Morphology of the Staminate Flowers in the Cucurbitaceae with Special Reference to the Evolution of the Stamen

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The importance of floral morphology in tracing evolution and natural affinity among flowering plants was realized by Eichler about a century ago. In 1875 he published his classic work *Blüthendiagramme* in which critical analyses of the morphology of flowers in a number of natural families were presented. At about the same time several French botanists like Naudin (1855), Van Tieghem (1875), and Baillon (1878, 1886) made similar attempts. Later Henslow (1891) contributed a valuable paper 'On the vascular system in floral organs and their importance in the interpretation of the morphology of flowers', whereas Goebel attempted to determine the significance of floral structures in his *'Organographie der Planzen'* (1890).

With the advent of modern equipment the problem has become more easily approachable and has been subjected to further critical study. During the last half century many botanists[2] studied floral morphology and attempted to interpret floral structures and their role in evolution.

Considering the family *Cucurbitaceae*, Naudin (1855) discussed its floral morphology and Pax (1890) made certain morphological observations on the stamens. A detailed taxonomic account of the family was given by Alfred Cogniaux (1881) in De Candolle's *Monographiae Phanerogamarum* and in Engler's *Pflanzenreich*. In 1894, Müller and Pax discussed the taxonomy and morphology of the Cucurbitaceae in Engler and Prantl's *Die Natürlichen Pflanzenfamilien*.

Engler (1936) treated the *Cucurbitaceae* as an independent family under the order Cucurbitales between *Dipsacaceae* (under Rubiales)

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[2] Arber, Engler & Prantl, Troll, Eames and MacDaniels, Thomas, Saunders, Joshi, Wilson, Grove, Thomson, Puri, Wilkinson, *et al.*

and *Campanulatae*. By comparison, Hutchinson (1926) placed it under the order *Cucurbitales* between *Achariaceae* (under *Passiflorales*) and *Begoniaceae* (under *Cucurbitales*), while Rendle (1925) put it between *Loasaceae* (under *Parietales*) and *Begoniaceae* (under *Cucurbitales*). Bentham and Hooker (1862–67) in *Genera Plantarum* placed it between *Passifloraceae* and *Begoniaceae*. Small (1913) referred it to *Campanulales* between *Asoraceae* (under *Aristolochiaceae*) and *Campanulaceae* (under *Campanulales*), while Britton and Brown (1898) followed Engler's view. This controversy about the systematic position of the *Cucurbitaceae* has now been resolved and the family is usually placed between *Passifloraceae* and *Begoniaceae*, an arrangement that has been adopted in Kew, Edinburgh, and other British herbaria.

The true morphological nature of the stamens of *Cucurbitaceae* is not yet clearly understood. The range of variation of the number of stamens and their structure, disposition, and modification are remarkable in this family. Cohesion, adnation, and reduction of the members are traceable in a number of genera. Usually, at least in the cultivated cucurbits, the number of stamens is three. Of these, two are bithecal[3] (bilocular or two-celled) and the third monothecal (unilocular or one-celled), as shown in Fig. 75. Each theca is two-lobed and each lobe contains a microsporangium hence two microsporangia are present in a theca. Therefore four microsporangia are present in each of the two bithecal stamens and two in the monothecal stamen. Generally each theca is thrice folded or convoluted so that in a cross section of a normal androecium with three stamens six cross sections of the thecae in each of the bithecal anthers and three cross sections of the theca in the monothecal anther, i.e. (6+6+3) or 15 transverse sections of the five loculi distributed among three stamens in a 2+2+1 arrangement would be expected (Figs. 3, 33, 46). As each loculus contains a pair of sporangia, a cross section of a normal three staminate androecium, passing through the middle of the anther, shows as many as 30 sporangia (Figs. 3, 33, 46).

Before dehiscence, however, the two contiguous sporangial cavities of a loculus become confluent into a single pollen sac due to the break down of the conjunctive tissue (sterile partition tissue) at the point just below the notch of the loculus between the two sporangia (Fig. 48). Since tetrasporangiate sporangia are the rule in flowering plants the two bithecal stamens in the family each with four sporangia, have been considered by some as complete and the other odd monothecal stamen with two sporangia a half stamen.

The following genera are predominantly three staminate:— *Apodanthera* (S. America), *Oreosyce* (W. & S. Africa), *Wilbrandia* (S. America), *Melothria* (cosmopolitan in S. America, tropical Africa, India and Malaya), *Dactyliandra* (tropical Africa), *Blastania* (W. India), *Muellerargia* (S.W. Malaya), *Pisosperma* (S. and E. Africa), *Toxanthera*

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[3]A theca is equivalent to a loculus which is often described as a cell. Usually in flowering plants an anther of a stamen has two thecae, each theca is two-lobed, and each lobe contains a microsporangium. Hence 4 microsporangia are found in a normal stamen. The description of a three-staminate flower in *Cucurbitaceae* is hence given as '*stamina 3, antherae una 1-locularis, ceterae 2-loculares*' (cf. Benth. et Hook., Genera Plantarum, 1862, I, 818–841).

(tropical Africa), *Kedrostis* (tropical Africa and India), *Corallocarpus* (tropical Africa and India), *Melancium* (S. America), *Edgaria* (E. Himalaya), *Trochomeriopsis* (Madagascar), *Cucurbitella* (S. America), *Dendrosicyos* (N. Africa), *Tumamoca* (C. America), *Cerasiocarpum* (E. India and Malaya), *Helmontia* (S. America and British Guiana), *Maximowiczia* (N. Africa), *Cucumeropsis* (W. Africa), *Posadaea* (S. America), *Dicaelospermum* (W. India), *Selysia* (S. America), *Schizopepon* (China), *Sicydium* (C. and S. America), *Pteropepon* (S. America), *Telfairia* (tropical Africa, Madagascar), *Edmondia* (S. America), *Acanthosicyos* (S. Africa), *Memordica* (cosmopolitan in Africa, Asia, and Australia), *Coccinia* (cosmopolitan in India, Africa, Malaya, etc.) occasionally five bithecal flowers develop in *C. cordifolia*, *Luffa* (cosmopolitan in Africa, Asia, and Australia), *Neoluffa* (E. Himalaya), *Bryonia* (Mediterranean Region), *Ecballium* (tropical Africa and Mediterranean Region), *Sphaerosicyos* (Africa), *Colocynthis* (tropical Africa, S. America, Mediterranean Region, India), *Cucumis* (tropical Africa, Mediterranean Region, India, Malaya), *Cucurbita* (cultivated), *Lagenaria* (cultivated), *Bryonopsis* (tropical Africa and Asia), *Benincasa* (E. Asia and Malaya), *Cionosicyos* (Jamaica), *Dimorphochlamys* (tropical Africa), *Biswaria* (E. Himalaya), *Herpetospermum* (E. Himalaya), *Gymnopetalum* (S.E. India and Malaya), *Trochomeria* (S. and E. Africa), *Eureiandra* (W. Africa), *Peponium* (tropical Africa), *Adenopus* (tropical Africa). In almost all three staminate flowers the thecae are variously convoluted.

The following genera are predominantly five staminate and have only one theca in each stamen—*Fevillea* (S. America), *Indofevillea* (E. India), *Anisosperma* (E. Brazil), *Alsomitra* (E. Australia, New Guinea), *Neoalsomitra* (India, Malaya), *Gerardanthus* (E. and S. Africa), *Hemsleya* (China), *Zanonia* (Malaya, China, India), *Siolmatra* (S. America), *Actinostemma* (India, China), *Gomphogyne* (India, China), *Thladiantha* (E. India, China), *Bambekea* (W. Africa). The thecae in five staminate flowers are usually erect or slightly bent and never convoluted.

Two staminate flowers are present in the following genera: *Anguria* (S. America, W. Indies, Cuba, etc.), *Guraniopsis* (S. America Peru, etc.), *Gurania* (S. America, Peru), and occasionally *Luffa* (*L. tuberosa* Roxb). The extreme case of flowers with a single stamen is known from *Cyclanthera* (S. America).

The position occupied by anther loculi (thecae) on the connective is also noteworthy. As noted above in the five staminate flowers they are erect, in the three staminate ones they are variously folded and vertically disposed. In *Sicyos* the loculi are folded and more or less horizontally disposed, whereas in *Cyclanthera* they are fused into a ring and horizontally placed. In *Cucurbita* the stamens are syngenesious.

The stamens of the *Cucurbitaceae* have been considered as two and a half by Gray, Heimlich, Saunders, and others because of the presence of monothecal stamens in three staminate flowers (Fig. 75). Others like Clarke, Britton and Brown, Small, Ridley, Gamble, *et al.*, described Cucurbitaceae as three staminate, whereas Willis, Wettstein, Torrey, and Warming along with others held the view that they are five staminate. The presence of the monothecal type of stamen in the family involved arguments in considering the bithecal stamens in three taminate flowers as complete (cf. Heimlich, Saunders) and the odd

stamen with one theca simply as half of a complete stamen.   In order to determine the real significance of these interesting structures, I undertook a thorough morphological study of the staminate flowers of some of the common genera.

MATERIALS AND METHODS

Eleven genera covering 14 species were studied.   They are: *Trichosanthes anguina* Linn., *Lagenaria leucantha* (Duch) Rusby, *Momordica charantia* Linn., *Luffa acutangula* Roxb., *Bryonia dioica* Jacq., *Cucumis melo* Linn., *Cucumis sativus* Linn., *Benincasa hispida* (Thunb.) Cogn., *Coccinia cordifolia* (Linn.) Cogn., *Cucurbita pepo* Linn., *Cyclanthera pedata* Schrad., *Cyclanthera explodens* Naud., *Thladiantha dubia* Bunge. Most of these plants were raised in green houses or in the open at Cambridge University Botanic Garden from seeds procured from India and other sources.   Besides specimens of almost all of these plants were brought from India preserved in formal acetic alcohol.   Flowers of *Bryonia dioica* were collected locally in Cambridgeshire.

Seeds were sown in late May or early June and flowering commenced by the beginning of September.   Fresh materials were fixed and killed in Belling's modification of Navashin's fixative (see Lee, 1937) except *Coccinia cordifolia*, specimens of which were brought from India preserved in FAA.

Serial microtome sections of male flower buds of different ages, were cut at 12–15 microns.   Light green dissolved in equal parts of clove oil and xylol or fast green dissolved in equal parts of absolute alcohol and clove oil and safranin in 50% alcohol were found suitable combinations.   Bismark Brown was used in certain cases.   Free hand sections of flower buds or flowers were examined whenever needed. Materials were often studied from fresh collections.

Position of floral members in relation to mother axis (Figs. 64–71) has been mostly determined in the field after observation of a great number of flowers from the same species.

For determining the course of vascular bundles from pedicel to different floral members, methods adopted by Sporne (1948) were found suitable.   Thick sections (T.S. or L.S.) from 5–2 mm. in thickness cut from the flower buds previously preserved in formal alcohol, were transferred to pure lactic acid in a test tube and the tube then kept for about half an hour in a boiling water bath or flask.   This makes the cellulose tissue transparent leaving the xylem elements opaque. The sections were then transferred in a watch glass and observed under the binocular microscope and dissections made while under observation. Air bubbles when present were removed under a vacuum pump.   Larger sections were then transferred in a square cell prepared over a slide by resinous[4] cement.   The cell is prepared by means of a hot iron rod. As usual they were mounted in pure lactic acid under square cover slips.

Round black rubber rings or thick glass rings fixed upon the slide

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[4]1.   Lanoline, anhydrous...................................4 parts.
   2.   Resin, powdered......................................8 parts.
   3.   Balsam, dry powder..................................1 part.
<div align="right">(after Sporne).</div>

by canada balsam, served the same purpose of the cement cell. The advantage in this case was that round cover slips could be used and be cemented in gold size by using a turn table. The method in short is— one surface of the rubber or glass ring is slightly painted with 'canada balsam' and then fixed upon the slide. The cell should not be used before the canada balsam hardens. After the canada balsam dries hard fill the cell with lactic acid, transfer the material in it, cover it by round cover slip and cement by gold size with the help of turn table. The smaller materials were mounted directly in grooved slides using lactic acid, round cover slip, and turn table as stated.

Most figures were drawn in a dark chamber with micro-projection equipment, whereas some were drawn with the aid of a camera lucida. A few are diagrammatic.

OBSERVATIONS

1. *Trichosanthes anguina*, snake gourd: Pedicel possesses 12 bicollateral bundles, placed more or less in two rings. The receptacle is formed by cohesion and adnation of calyx and corolla. At the base of the receptacle 15 bundles are present at different distances from the center. Of these the ten outer bundles pass alternately as traces for sepals and petals. Of the remaining five internal trace bundles one remains free and the other four run in 2 pairs. One of these pairs fuses at the base and the other at midway in the receptacle. These five bundles form the bundles of the stamens in 2+2+1 disposition. Each of the two fused bundles passes into the filaments of bithecal stamens whereas the odd one supplies the monothecal (Fig. 1). Higher up in the anther region the fused bundles bifurcate again. Hence they are free at the bottom, fused at the middle, and free again at the end. As the thecae are three folded, 6+6+3 microporangial sacks are found in transverse section (Fig. 3). The filaments of the fused stamens are wider than is that of the single one (Fig. 2). The endothecium contains uninucleate cells and the conjuctive tissue is made up of a few, layered, elongated cells which are very weak, as indicated by their crumpled nature.

Development of sporangium: The primordial cells of each theca are similar but later differentiation into dermal and sporogenous tissue is marked and the epidermal cells enclose the potentially sporogenous tissue. Then each theca gradually becomes slightly two lobed and a group of three to four archesporial cells develops under the epidermis of each lobe. By periclinal divisions of these archesporial cells primary parietal and sporogenous cells are formed. The former again divide periclinally and ultimately four parietal layers of cells are formed. The innermost parietal cells construct the tapetum.

The tapetal cells are at their maximum development during the formation of spore tetrads. The conjunctive tissue, in transverse section, shows three to four long rows of cells between the two groups of sporogenous tissues, the cells of which are more or less elongated. At the upper end they terminate associated with a group of four or five small cells (stomium cells) occupying the notch between the lobes of the theca.

Without further division the primary sporogenous cells become the

spore mother cells. In longisection the sporogenous tissue develops in a convoluted fashion. After the reduction division the spore tetrads lie in the much enlarged microsporangium.

The middle layers of parietal cells are subjected to great tension during the development of the sporangium and enlargement of the cells of the tapetum and the endothecium. They thus appear stressed and flattened and later they disorganize after the development of microspore tetrads, the remnants of which persist and form the inner lining of the sporangium just below the endothecium. The endothecium is formed from the inner parietal layer and almost encircles the pollen sac except at the region of the stomium. When the theca is mature the epidermis has almost disappeared and has been replaced by much ribbed (fibrous) endothecium cells.

2. *Lagenaria leucantha*[5] (Duch) Rusby, bottle gourd: The pedicel has 12 bundles arranged in 2 rings. At the base of the receptacle the bundles increase and almost coalesce (Fig. 16). Three trace bundles per sepal and one bundle per petal are noticeable. The sepal main and petal main lie 18° apart at slightly higher levels. The inner surface of the receptacle (Fig. 5) gives off 5 stamen bundles which enter the filaments in a $2+2+1$ disposition. The pair of bundles of the bithecal stamens remains distinct all through the filament but fuses in the region of the anther. At this point they branch again and supply the developing stamen loculi both ways. The odd stamen with its single bundle remains distinct throughout (Figs. 6–14).

In certain flowers 4 stamens are found. In these cases the bundles are arranged as follows, $2+1+1+1$, the first stamen being bithecal and the others monothecal.

The conjunctive tissue of 7–10 layers breaks, when the stamen matures, at the point of the stomium whereby the two sporangia become confluent (Fig. 4a). The endothecium and conjunctive tissue are quite fibrous. The staminal trichomes are grey. The traces of the pistillodium are much weaker and anastomosed (Fig. 5).

3. *Momordica charantia* Linn. The original number of bundles in the pedicel (about nine) ·increases to about fifteen or twenty at the receptacle-base, where they are disposed roughly in two rings without coalescing. A glandular three lobed pistillodium is present in the center of the receptacle with a number of weak bundles. Of the ten outer bundles, five go to the sepals and five to the petals. The sepal and petal laterals are formed by branching of the mains. As in the

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[5]*Lagenaria leucantha* (Duch) Rusby $(=L.\ vulgaris$ Ser.).

ABBREVIATIONS USED: S—sepal; S T—sepal trace; P—petal; P T—petal trace; Stb—stamen bithecal; Stb T—stamen bithecal-bundle; St m—stamen monothecal; Stm. T—stamen monothecal trace; Pi—pistillodium; Pi T—pistillodium trace; Pd—pedicel; Pd B—pedicel bundle; Stl—stele; R—receptacle; R T—receptacle trace; E—epidermis; En—endothecium; Sp—sporangium; C T—conjunctive tissue; Pn—pollen grain; G H—glandular hair; T—tapetum; F—filament; C—connective; M 1—middle layer of cells of the sporangium wall; H—hair; Pn t—pollen tetrad; St—stomium.
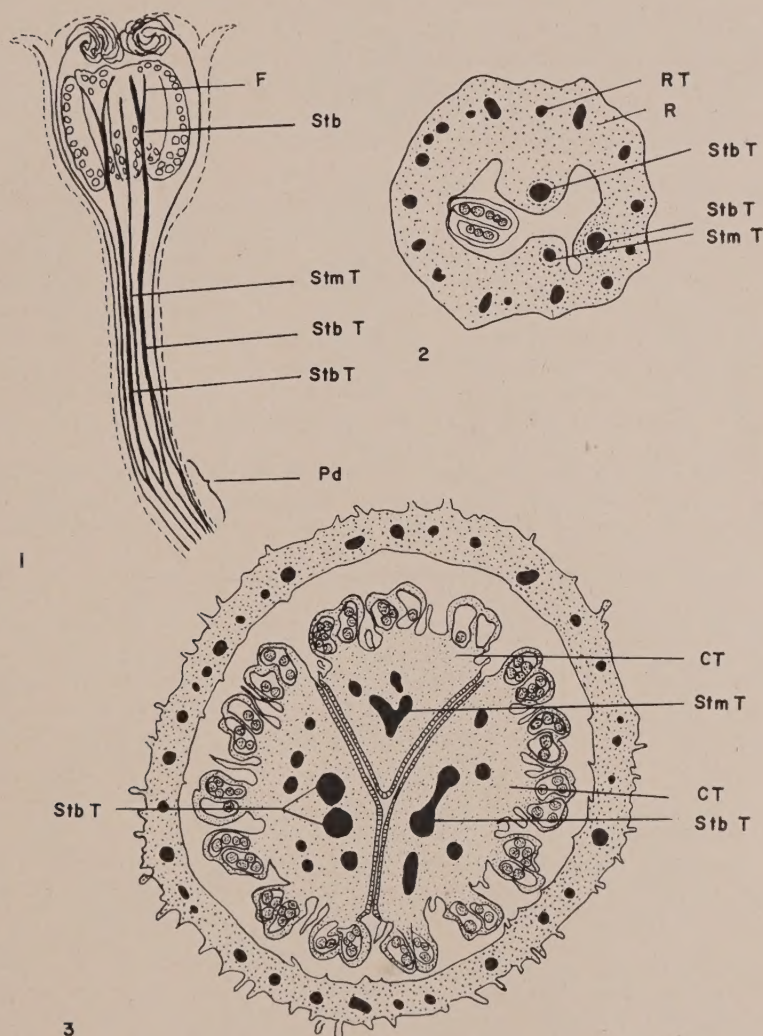
Trichosanthes anguina Linn., FIG. 1.—Longisection through flower bud showing traces for sepal, petal, and stamen, fusion of two traces for each bithecal stamen and forking (f) of the fused trace towards the end of the connective. × 10. FIG. 2.—Cross section of very young bud through the lower part of the receptacle showing traces for three stamens; two traces of bithecal stamens are larger than the third monothecal one. × 30. FIG. 3.—Cross section of somewhat older bud at an upper level showing three stamens with 6+6+3 thecal sections; two traces of a bithecal stamen not yet fused, staminal traces branching in the connective. × 25.

preceding species, the five inner bundles destined to supply the stamens are arranged in a 2+2+1 order at the receptacle-base where they bend round the three lobed pistillodium (Figs. 17, 18). A pair of bundles of the bithecal stamen fuses at the base of the anther and then branches laterally (Fig. 19). The innermost fused bundles go to the pistillodium. The tapetal cells were detached from the sporangial wall and abutted closely the sporogenous tissue. Pollen grains are finely warted.

4. *Luffa cylindrica* Roem., sponge luffa: The pedicel contains 12 bundles which increase from 18–20 by branching at the base of the receptacle. Here they are arranged in two rings with roughly five in the outer ring and the rest in the inner. These bundles do not fuse. They branch higher up where the branches surround the pistillodium more or less in a circle (Figs. 20, 21) and other smaller bundles are found inside the pistillodium. As in the preceding species, the outer bundles go to the sepals and petals: 15 to the sepals and 5 to the petals. The inner five bundles supply the three stamens as indicated before.

The stamens in *Luffa cylindrica* are interesting as they fluctuate between five and three in the same plant. Fusion of stamens is not an obligatory feature, as often four of the five stamens are united below in a couple of pairs but free above. The stages of the fusion of two stamens are clearer in this species (Fig. 21). A pair of bundles fuses in the connective (Fig. 15).

At the receptacle three lobes project into the space of the tube where 2+2+1 bundles are seen above the base. The filaments of the bithecal stamens also arise at different levels from the receptacle. The filaments are much lobed when young. The tapetal cells are closely attached to the endothecium and the two layers of the tapetal cells of the two adjacent sporangia form the conjunctive tissue. The conjunctive tissue is very thin from base to apex. The original sterile

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EXPLANATION OF FIGURES

Lagenaria leucantha (Duch.) Rusby, FIG. 4.—Longisection of flower bud show-ing traces for stamens. × 10; 4a—cross section of a theca showing two sporangia. × 20. FIG. 5.—Longisection of flower bud showing the vascular skeleton, i.e., the traces for floral members; two staminal traces united in the connective. × 1.3. FIGS. 6–9.—Cross section of the flower bud at different levels, showing traces for the bithecal and monothecal stamens; Fig. 6, × 5; Fig. 7, × 7; Fig. 8, × 6; Fig. 9, × 60. FIG. 10.—Cross section of the same bud at a still higher level showing filaments of three stamens; filaments of the two bithecal stamens have two traces in each, while filament of odd stamen has one trace; the traces in the broader filaments (of bithecal stamens) are not at equal distances in both, though they are at the same level of the flower; their fusion takes place at different levels. × 9. FIG. 11.—Cross section of the flower bud with sporangia. Traces in one filament of a bithecal stamen have fused and in the other are separate; branching trace of monothecal stamen is shown branching. × 7. FIGS. 12–13.—Cross section of very young flower bud shows traces for stamens passing through the receptacle in 2+2+1 arrangement. × 20. FIG. 14.—Cross section through an older flower bud with four stamens; only one is bithecal with two traces, whereas the others are all monothecal. × 13. FIG. 15.—Flower bud at a higher level showing aestivation. × 20. FIG. 16.—Arrangement of bundles from the pedicel to the receptacle, (i)—at the base of the pedicel, (ii) higher up in the pedicel, (iii) at the base of the receptacle, (iv-vi) at different levels of the receptacle showing the siphonostele (diagrammatic).

17

18

19

Stb T

R

Stm T

Stb T

Stb T

R

Stm T

P

S

ST

Stb T
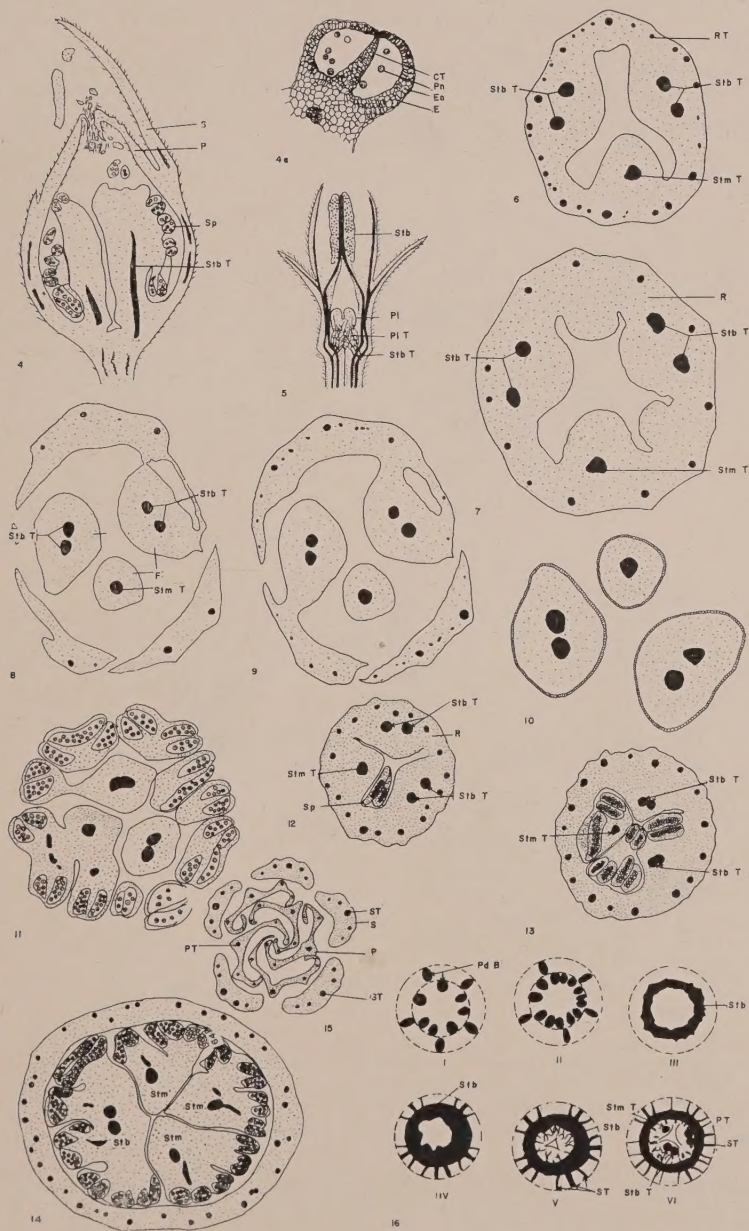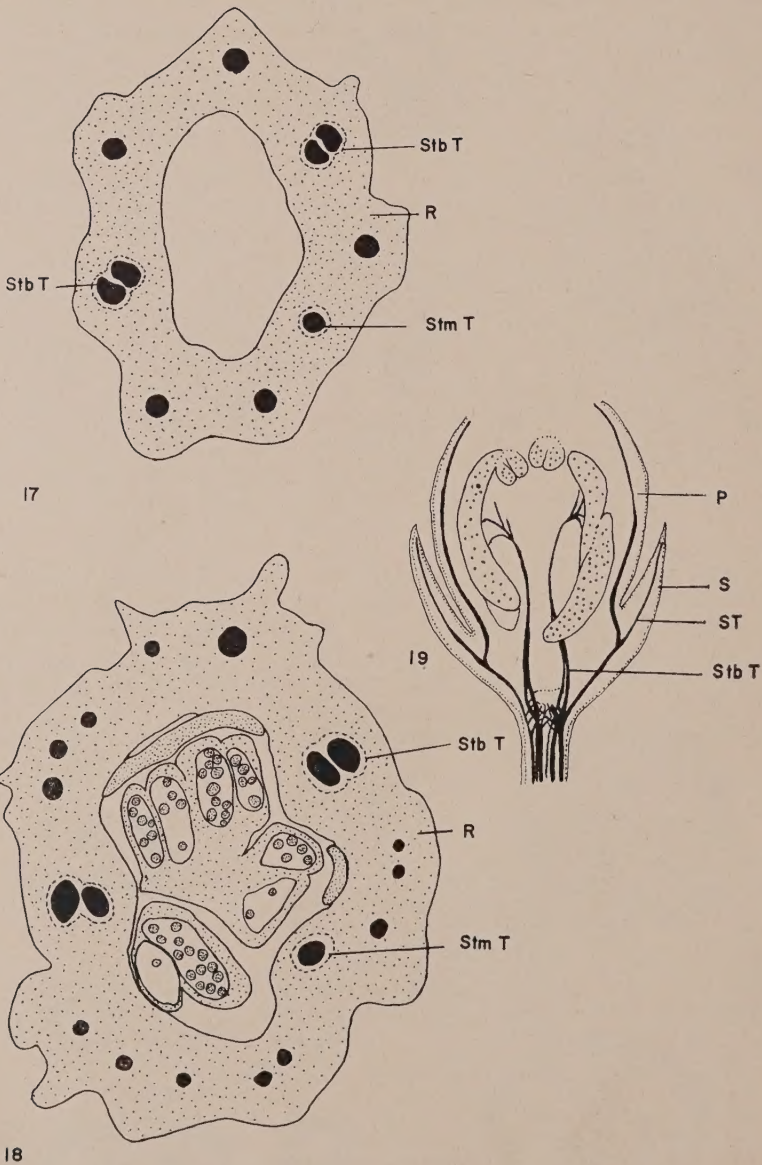
Momordica charantia Linn., FIGS. 17–18.—Cross section of flower bud showing receptacle with traces of stamens.   × 30.   FIG. 19.—Longisection of flower bud showing traces for floral members; two pairs of traces for bithecal stamens fuse in the receptacle and branch above.   × 8.

conjunctive tissue is simply pressed to form a membranous wall and no cellular structure is traceable (Fig. 21A). In the floral bud (ptyxis) the sepals are valvate and the petals are imbricate (Fig. 23).

5. *Luffa acutangula* Roxb., angular sponge luffa: It possesses the same pattern of vascular arrangement as does *L. cylindrica*. But in this species the stamens are definitely three, two bithecal and the other
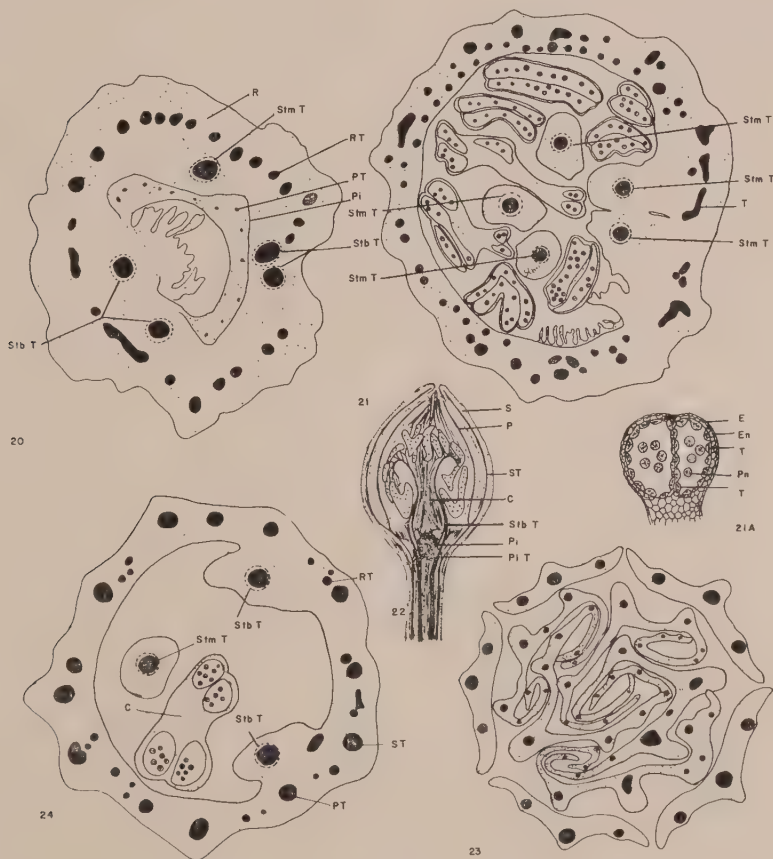
Luffa cylindrica Roem., FIG. 20.—Cross section of flower bud showing traces for stamens within dotted circles and traces at the receptacle, pistillodium, and lobed filament. × 20. FIG. 21.—Cross section of same bud, at a higher level; three filaments are free from the receptacle, while two are still attached to it, and fused at the base. × 15. FIG. 21a.—Cross section of a theca. × 40. FIG. 22. Longisection of flower bud showing traces of floral members (lactic acid treatment), fused traces of two bithecal stamens, and sepal main branches before leaving receptacle. × 5. FIG. 23.—Cross section of bud at a higher level showing aestivation. × 17.

Luffa acutangula Roxb., FIG. 24.—Cross section of flower bud showing orientation of staminal traces; two traces in the receptacle are slightly larger than the third which is free from receptacle; many traces are present in receptacle. × 15.

monothecal, i.e., fusion is obligatory in the bithecal stamens. The filaments are not lobed (Fig. 24). In this respect *Luffa acutangula* is phylogenetically more advanced than *L. cylindrica* (see discussion).

6. *Bryonia dioica* Jacq., bryony: From a sort of dissected siphonostele formed at the base of the receptacle by about 20 bundles 5 x 3 = 15 bundles go to the sepals and 5 x 1 = 5 to the petals.

The stamens do not arise at equal distances from one another. The two bithecal stamens arise at an angle of 180°, i.e., one opposite the other. However the odd one is closer to one of them but never at equal distances from them. In the receptacle two series of trace bundles are present, one series running through the outer surface and the other through the inner. Of these, five larger bundles in 2+2+1 arrangement lie towards the inner surface (Fig. 25). These are the bundles for the stamens. The pairs of bundles fuse at different levels of the receptacle. The pair of bundles in the bithecal stamen remains united all through the filament but the bundles separate before passing into the lobes of the anther. When old the conjunctive tissue breaks before the pollen is discharged and the sacs become confluent. No fibrous band was observed in the endothecium (Fig. 25A). The conjunctive tissue is spongy in nature. At different levels the filaments protrude from the receptacle into the tubular space, as they are much broader at the base.

7. *Cucumis melo* Linn., the melons: The pedicel has 10 bundles arranged in a single ring. After further branching the bundles fuse at the receptacle forming an irregular broad ring (siphonostele). From the outer surface of this ring 3 traces enter each of the sepals and, alternating with these groups of three bundles, a trace bundle enters a petal as main. As in *Lagenaria*, from the inner side of the ring bundle-traces enter in 2+2+1 arrangement the two bithecal stamens and the monothecal one (Fig. 27–29). The glandular pistillodium receives a number of weaker and shorter bundles from the innermost part of the vascular cylinder (Fig. 27).

The cells of the filaments are spongy and many swollen yellow trichomes develop from the wall of the filaments. The sporangia develop symmetrically on both sides of the conjunctive tissue which is 3–2–celled in thickness. The endothecium is fibrous. At maturity the two bithecal stamens may separate and five stamens may thus result. Under favorable conditions the sterile pistillodium may develop into a fertile pistil and hence bisexual flowers are formed. This has been observed in var. *superlative* cultivated in the Royal Botanic Garden of Edinburgh. The three stamens which arise from the base of the receptacle clasp the ovary.

8. *Cucumis sativus* Linn., cucumber: The vascular pattern is similar to that of *C. melo* (Figs. 30–33). Some flowers however develop four stamens, 2 bithecal and 2 monothecal, with bundles arranged in a 2+1+1+1 fashion. Of the stamens possessing a single bundle one is bithecal and the other two are monothecal. This bithecal stamen with a single bundle is a case of reversion to ancestral habit. This feature is occasionally found in other genera like *Lagenaria*, *Luffa*, etc. As the

conjunctive tissue is greatly subjected to great stress and strain by the developing sporangia cellular structure may break down in the mature stage and a thick membranous wall is formed which demarcates the sporangia.

9. *Benincasa hispida* (Thunb.) Cogn., white gourd: At the initial stage three sepal mains and a petal main are present in this species. Two trace bundles are present in each of the bithecal stamens and a single bundle is present in the monothecal one. The two trace bundles in the four sporangiate stamens run parallel along the whole length of the filament and then fuse in the anther near the middle of the con-
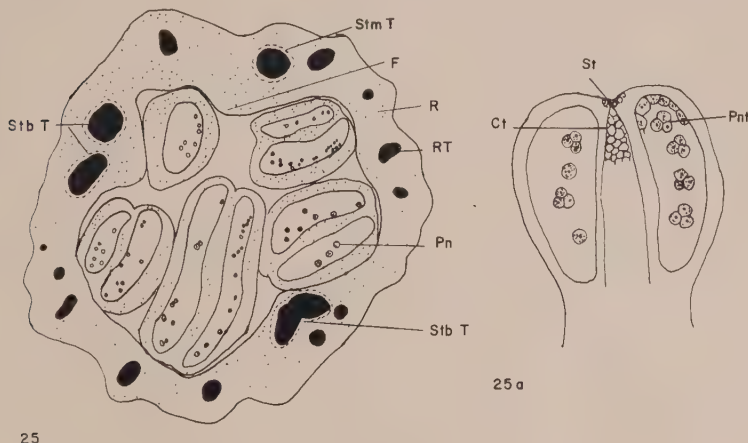
Bryonia dioica Jacq., FIG. 25.—Cross section through flower bud showing five stamen traces (in 2+2+1 arrangement), two traces of a bithecal stamen about to fuse, and trace of odd stamen on one side; all these traces are imbedded in the receptacle; receptacle is lobed ultimately separating into filaments. × 30. FIG. 25a.—Cross section of theca showing two sporangia and pointed conjunctive tissue touching the stomium cells. × 60.

nective but separate again at a higher level. At the beginning each theca shows a mass of small meristematic cells. Gradually it becomes slightly two lobed and 3–5 archesporial cells occur below the epidermis in each sigmoid lobe. The conjunctive tissue breaks down at the apical region either simultaneously with the disintigration of the sporangium wall or a little earlier.

10. *Coccinia cordifolia* (Linn.) Cogn. The 10–11 vascular bundles in the pedicel are arranged roughly in two rings. The bundles increase by branching at the floral receptacle. The sepals are valvate and petals imbricate in aestivation (Fig. 41b). Three traces per sepal and one per petal were observed. The central cavity of the receptacle is soon filled up by three filaments, two of which are slightly thicker than the third. The filaments are triangular in cross section with one or two lobes on the outer side. No bundle trace is present in the filaments at the basal region and here the filaments remain detached from the

receptacle wall (Fig. 38). They, however, fuse with the receptacle at a higher level (Fig. 39) where two trace bundles from the receptacle opposite each larger filament approach and finally enter the filament. A single trace bundle enters the third filament. Filaments disconnected from the receptacle below and fused above are a characteristic feature of this species. The two bundles of each of the bithecal stamens fuse in the filaments at different levels. The flowers possess three bithecal stamens and the thecae are thrice folded hence $6+6+6=18$ sections of the thecae containing 36 sporangia are found (Fig. 40, 41). It is interesting to note that of three bithecal stamens only two receive two bundles each and one receives a single bundle (Fig. 73, xii). Rarely five bithecal stamens are found in this plant (cf. Chakravarty & Sen Gupta, Bull. Bot. Soc. Beng., 1951, *5*, Fig. 23), each stamen having a single bundle. The conjunctive tissue which is few-celled in thickness at the initial stage is subjected to great pressure due to the expansion of the sporangia on both sides. As a result the cells become much elongated and ultimately are crushed and what remains of the conjunctive tissue is only a membrance formed by the pressed cells (Fig. 41A).

11. *Cucurbita pepo* Linn., pumpkin: The pedicel has 12 vascular bundles arranged in two rings. The bundles branch as they go up in the receptacle. The bundles fuse in the receptacle and then 15 bundles from five groups of three traces each enter a sepal and three bundles enter as petal mains (Fig. 43). Internally from the fused vascular cylinder larger traces in $2+2+1$ arrangement branch off and enter the stamens (Figs. 44, 45, 52) while many weaker and shorter traces pass to the pistillodium (Fig. 49).

A thick membranous coat encircles the sporangium. This membrane is formed by coalescence of the outer wall of the tapetal cells with the outer wall of the conjunctive tissue or the inner wall of the endothecium. The pollen grains are spinous (Fig. 48). Peculiar elongated multicellular glandular hairs develop from the inner surface of the receptacle (Fig. 54a) in addition to ordinary hairs.

12. *Cyclanthera pedata* Schrad. The pedicel contains 3–5 bundles (Fig. 57a). At the base of the receptacle they fuse into an almost solid cylinder from which 10 traces depart at an angle of 36° apart, one bundle per sepal and one per petal. In some cases two of these strands may have a common origin, i.e., when the original bundle number is 8 or 9. When the number is 8, two of these bundles fork or, when it is 9, only one forks, so that the ultimate number is always 10. The stele of the pedicel branches at a higher level (Figs. 57, 59). On close observation it becomes apparent that the single annular anther is the product of fusion of three anthers (Figs. 55, 56). The single stamen in this species is therefore nothing but the fusion product of three stamens, two with larger anthers than those of the third (Fig. 55). The fused thecae are horizontally placed on the fused filament and the loculi are annular with one confluent pollen chamber borne upon another as if two life-belts (buoys) were placed one above the other demarcated by the partition tissue (conjunctive tissue). To the naked eye the fusion appears to be complete, but under the microscope the

partition between the loculi is evident. Partial or complete partition between the junctions of two anthers is often traceable (Figs. 55, 56). However, the original 2+2+1 bundles of the stamens are not traceable. The stele of the receptacle is triangular and continues to the external apex of the floral axis. The conjunctive tissue of the sporangia is 5–4–celled in thickness. The pollen is smooth and usually trilobed.
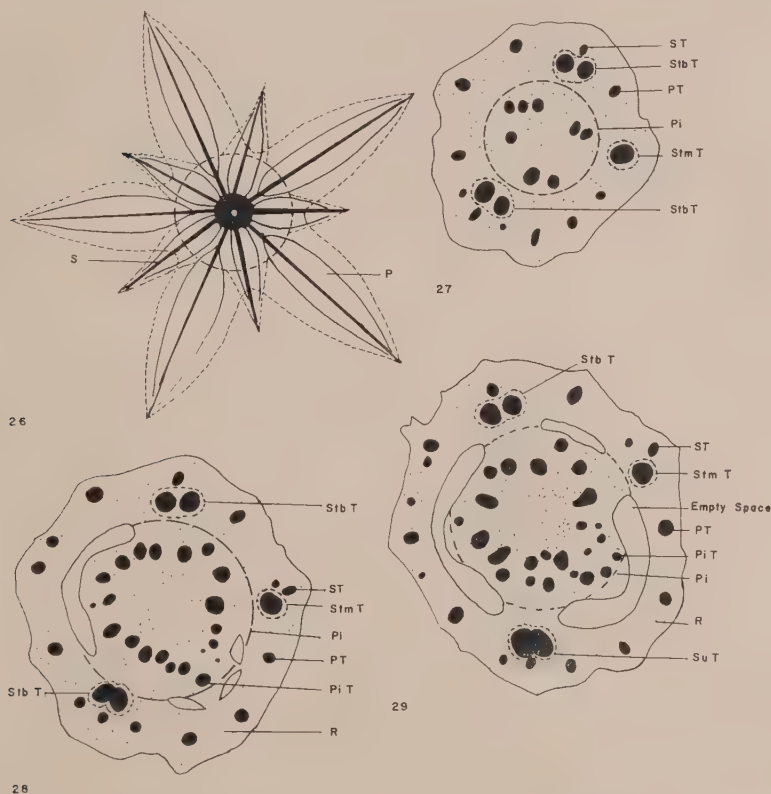
Cucumis melo Linn., FIG. 26.—Vascular plan of male flower (semidiagrammatic). FIG. 27.—Cross section of flower bud from basal region, showing traces of floral members and central pistillodium with traces. × 18. FIG. 28 same, but at a higher level showing separation of pistillodium from receptacle and circular arrangement of traces of pistillodium; stamen traces are about to fuse in one bithecal stamen. × 18. FIG. 29.—Same, but at a still higher level showing the increase in number of traces of pistillodium and its gradual separation from receptacle. × 18.

13. *Cyclanthera explodens* Naud. The pedicel has one bundle. Traces for sepals and petals are arranged as in the preceding species. The three antheral structures are clearly recognizable in this case. The vascular pattern of the flower is almost identical with that of the preceding species. The flower is very small, ±.5 mm. in diameter (cf. *C. pedata*, ±1 mm. in diam.).

14. *Thladiantha dubia*. The pedicel has 10–12 bundles (Fig. 60) surrounded by a two-layered pericycle. The bundles increase to 10–16–18 at a higher level and are arranged almost in two rings. Actually the bundles do not fuse at the base of the receptacle but are crowded. A glandular pistillodium develops in the center of the receptacle. Each of the ten lobes in the receptacle which develop into sepals and petals receives a trace bundle whereas various smaller bundles supply the pistillodium.   Five filaments emerge as projections of the receptacle internally and in each of these filaments a single trace is clearly seen. Of the five filaments four lie closer as if in pairs, whereas one remains apart (Fig. 61).   The two trace bundles of the closer filaments seem to arise from a common fused trace but on careful examination these traces are found running closer to one another through the inner surface of the receptacle and touching at a point before emerging from the receptacle as traces for two stamens (Fig. 13).   The filaments occupy about one-half of the inner space of the receptacle.

The five stamens are free and each bears one theca.   Unlike those of other species, the sporangia are asymmetrical.   They develop at different levels at the base of the anther (Fig. 62).   The conjunctive tissue is somewhat tortuous especially towards the upper region. The sporangia are beaked and more or less overlap one another.   The sterile tissue gradually tapers upwards.   The endothecium does not show any fibrous bands.   The outer wall of the pollen grain is transversely striated and looks as if minutely warted (Fig. 62A).

VASCULAR GROUND PLAN OF THE FLOWER OF THE CUCURBITACEAE

As I could not fully agree with the floral diagram as given by Eichler (*loc. cit.*) and because the relationship of the different floral members with the main axis has considerable importance in taxonomic classification, I studied particularly the relationship of the floral axis with the stamens and other organs of the flower.

The position of the floral members, especially that of the stamens, in relation to the main axis has been determined by examination of the growing point.   Due to the twinning nature of the shoot the position of the main axis changes considerably at different distances of the shoot.   The geometrical axis was determined by taking the terminal

Cucumis sativus Linn., Fig. 30.—Longisection of flower bud showing traces for floral members.   × 4.   Fig. 31.—Cross section of flower showing traces for stamens in 2+2+1 arrangement in receptacle.   × 20.   Fig. 32.—Cross section of same bud at a higher level showing fusion of traces of two bithecal stamens recognizable by their larger size and projection of filaments from receptacle, staminal trichomes and thecae hanging below attachment of filament.   × 20.   Fig. 33.— Same bud at a still higher level showing three stamens with (6+6+3) sections of the thecae.   Stamen traces are recognizable by their size.   Innumerable traces present in receptacle.   × 20.   Figs. 34–36.—Cross sections of flower bud with four stamens.   In Fig. 34 one trace (fused) is larger than the other.   In Fig. 36 two stamens are bithecal having 6 cross sections of thecae each and two are monothecal with 3 cross sections of a theca in each.   Of these, stamens (1) and (2) are monothecal with suppression of a theca in each; (3) and (4) are bithecal; stamen (3) with a single trace is a reversion to original bithecal habit (cf. Fig. 73, xii), whereas (4) has two fused traces and is therefore a compound stamen. Stamens (3) and (4) are homologous but (3) is analogous to (1) and (2).   × 20.
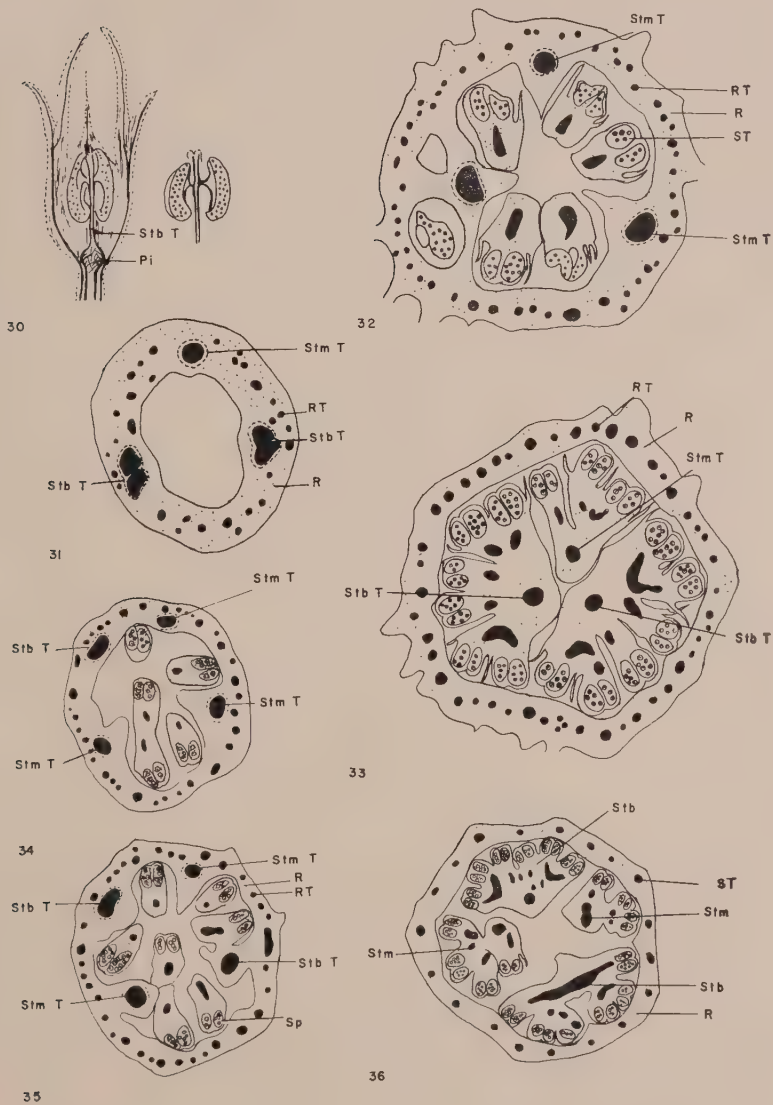
axis of an inflorescence or of a flowering shoot. In a shoot crowded with a number of flowers the axis was cut transversely without disturbing the flowers and a fine needle inserted just at the center which now represents the geometric mother axis. The determination of the exact position of the main axis with the flower is a painstaking job and to arrive at a satisfactory result a great number of flowering shoots was examined. It is often difficult to ascertain the position of the sepal or the petal which is just opposite the young axis, as a slight distortion of the flower or the axis may change their relative position considerably. The flower and the axis should not in the least be disturbed. Open flowers with long pedicels are useless as pedicels like stems may twist. In spite of the difficulty of the task, there is a great advantage in this family to check the position of the sepal or the petal by indirect method after determining the position of the stamens with the axis. It is easier to ascertain the relative position of the stamens with the axis, as in most cases three stamens are present and arranged in a circle in the bud. A section through the young flower bud immediately determines the position of the partition between the contiguous stamens in relation to the axis. Their angular divergences can also be easily measured. Once the staminal position of the flower with respect to axis is found it is easier to determine the position of the other members by drawing a vascular floral plan (Fig. 64–71).

The vascular ground plan was studied and diagrams were prepared for the following: *Trichosenthes anguina, Lagenaria leucantha, Cucurbita pepo, Memordica charantia, Luffa cylindrica, Cucumis sativus, Cucumis melo, Benincasa hispida, Cyclanthera pedata* and *Cyclanthera explodens.*

The floral members were placed in circles as they occur in nature. The innermost circle represents the androecium. In most of the species examined the stamens are three in number—one monothecal and the other two bithecal. In a cross section of the male flower bud they are found in a circle closely applied to one another with a line of separation between two adjacent stamens. The separation lies almost in a straight line. The smaller odd stamen which dimensionally is half of the bithecal stamen may be considered as the minor sector and the two larger ones as major sectors of the staminal circle. Geometrically the two major sectors and the minor sector complete a circle when symmetrically arranged. The minor sector (the odd stamen) subtends an angle of 72° at the center of the floral axis and each of the two major sectors (the larger stamens) therefore subtends an angle of 144°. The position of the odd stamen changes in relation to the axis in different genera. Once the position of the odd stamen is determined, the position of the bithecal stamens can be automatically ascertained because they are symmetrical. The angle of inclination of the bisector or median (OP) of the odd stamen on the axial line (OO') (imaginary line drawn by joining the organic mother axis with the floral axis) has been measured.

O—Center of the floral axis.

O'—Center of the mother axis.

OP—Bisector or median of the odd stamen AOB (minor sector) subtending an angle θ (72°) at the center of the floral axis.

AOC—A bithecal stamen (major sector) subtending an angle (144°) at the center O.

BOC—The other bithecal stamen (major sector) subtending an angle (144°) at the center O.

O—Angle between OA and OB, bisected by OP the median.

OO'—Axial line, obtained by joining floral axis O with the mother axis O'; OO' is produced bothways to X and X'.
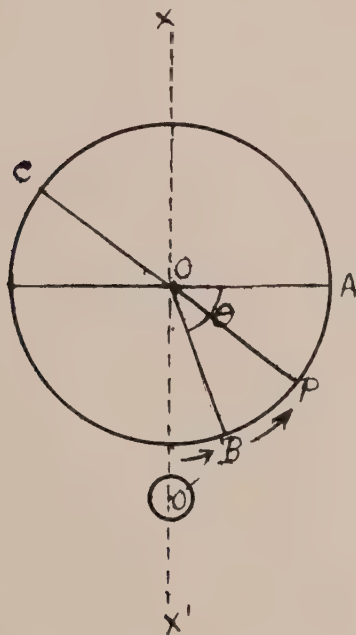
FIG. 37.—Circle showing two major sectors (larger stamens) subtending angles of 144° and one minor sector (odd stamen) subtending an angle of 72° at the center of the floral axis.

Angular measurement of the bisector of odd stamen is calculated in the positive or counterclockwise direction assuming OP placed along the axial line OO' at the initial stage, i.e., OP is at 0° with XCX'.

The position of the stamens in relation to the axis seems to have considerable taxonomic importance, as it is a fixed character in a genus or in a group of genera.

TABLE 1

| Type	Species	Angular divergence of OP with XOX'	Mother axis S or P opposed	Diagram	Remarks
I	*Trichosanthes anguina*	72°	Sepal	Fig. 64	
II	*Cucurbita pepo* and *Lagenaria leucantha*	180°	Petal	Fig. 65	Eichler placed sepal opposite M-axis. This view is not accepted here.
III	*Momordica charantia*	0°	Sepal	Fig. 66	
IV	*Luffa acutangula* and *Luffa cylindrica* (3-staminate)	0°	Sepal	Fig. 67	
V	*Luffa cylindrica* (5-staminate)	——	Sepal	Fig. 68	Each stamen subtends an angle 72° at the center and one nearest to M-axis is bisected by the axial line
VI	*Cucumis sativus* and *Cucumis melo*	216°	Sepal	Fig. 69	
VII	*Benincasa hispida*	——	Petal (?)	Fig. 70	All stamens are bithecal but the bundles are distributed as 2+2+1
VIII	*Cyclanthera pedata*	——	Sepal	Fig. 71	United into a single stamen but basically three

Coccinia cordifolia (Linn.) Cogn., Fig. 38.—Cross section of flower bud showing three ventrally lobed filaments free at center and traces of the bithecal stamens fused in one case and separate in the other. × 18. Fig. 39.—Cross section of same bud at a higher level showing fusion of filaments with receptacle; traces of a bithecal stamen not yet fused. × 18. Fig. 40.—Same, at a still higher level showing section of anthers of three stamens with 6+6+6 cross sections of the thecae; all are homologous but one with single trace which is analogous to monothecal stamen. × 12. Fig. 41.—Cross section of same bud at a still higher level showing fused traces of bithecal stamens and separate trace of monothecal one, receptacle with many traces leading to sepals, and conjunctive tissue made up of membranes of tapetal layer of cells and not of specialized sterile tissue. × 17. Fig. 41a.—Sporangium showing details. × 34. Fig. 41b.—Aestivation of petals. × 20.
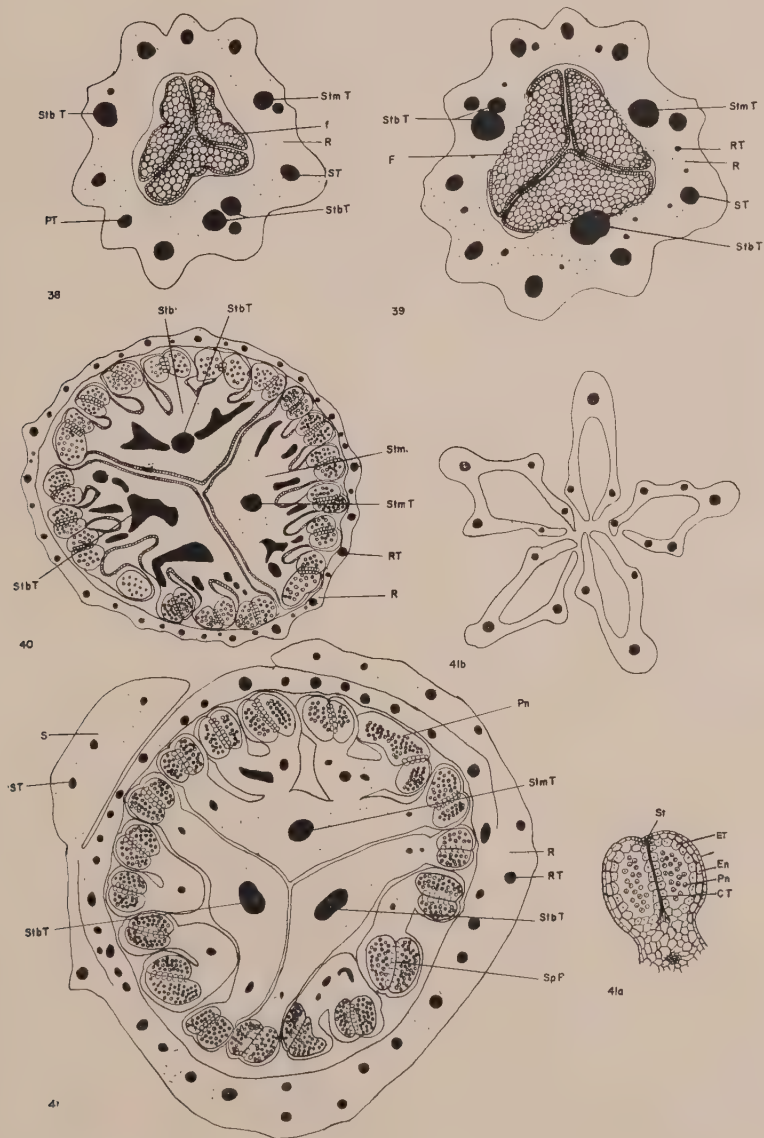
DISCUSSION

The pedicels of the flowers of the species examined show the anatomical features of the shoot. In most cases the bundles are bicollateral but a visible cambium between the xylem and the phloem is often absent. Fischer (1894) also mentions bicollateral bundles without cambium in certain species. As the inner phloem often decreases in mass or disappears, in many cases, toward the apex, the bundles are all collateral in nature. In *Cyclanthera explodens* the vascular system of the pedicel near the receptacle is of the form of a solid cylinder with xylem surrounded by phloem. Throughout the pedicel the bundles are generally arranged in two circles. Even when they do not appear to be arranged in two circles, they are found at different distances from the epidermis. In fact, they are often found in a single distinct ring (*Coccinia cordifolia, Cyclanthera pedata, Cucumis melo*, etc.).

In all species of *Cucurbitaceae* examined the receptacle shows both cohension and adnation. In most cases (except *Trichosanthes, Momordica, Luffa,* and *Coccinia*) the bundles fuse at the receptacle-base forming a siphonostele with traces radiating to sepals and petals. In general 15 traces in five groups of three go to each sepal, and one trace alternating with a group of sepal traces goes to each petal. In *Momordica, Coccinia*, and *Luffa* a sort of dissected siphonostele is formed in the receptacle from which traces the floral members branch out. In *Cyclanthera* the bundles in the pedicel form a solid cylinder from which ten traces (5 per sepal and 4 per petal) radiate. In all species examined the stele at the base of the receptacle is the center of distribution for all traces supplying calyx, corolla, androecium, and gynoecium. Traces for stamens and pistillodium (when present) come from the inner side of the stele and run through the inner surface of the receptacle, while sepal and petal traces pass through the outer five larger traces in $2+2+1$ arrangement to supply three stamens. Traces for the pistillodium are far more numerous but they are smaller

and weaker. These traces are arranged in a circle in the outer wall of the pistillodium, whereas some are also found scattered within.

The true morphological nature of the stamens of *Cucurbitaceae* has not been fully understood, although from time to time attempts have been made to explain the monothecal nature of the stamen (the odd stamen). In this family the stages of transition of the floral members are very interesting. The pentamerous construction of the flower has been modified in androecium and gynoecium. Calyx and corolla do not show any change in reduction of their parts but they show both cohesion and adnation. In the receptacle the members of the calyx and the corolla are not only united but are fused with the neighboring whorls.

Most genera have three stamens, two of which are bithecal and the other is monothecal with two sporangia in each theca. Hence a bithecal (two-locular) stamen produces four sporangia, whereas a monothecal stamen produces only two sporangia. The nature of stamens has been variously interpreted, the monothecal stamen being regarded as half a stamen and the two bithecal stamens as complete. Thus Gray (1908) and Heimlich (1927) along with others regarded the stamens as two and a half, whereas Bentham and Hooker (1868), Clarke (1879), Britton and Brown (1913), Small (1913), Ridley (1922), Gamble (1935) and a number of others described them as three, and Warming (1890), Willis (1919), Wettstein (1924), Torrey (1938–40), Saunders (1939) et al. considered five as the basic number of stamens. Saunders is still of the opinion that this basic number has never been met in any living members. According to her interpretation, all 5 stamens present in the species investigated are half stamens derived by splitting of two complete stamens. Hence she too supports the $2\frac{1}{2}$ staminate nature of Cucurbitaceae.

I have already shown that most of the about 90 genera belonging to this family (*Melolothria, Cucumis, Memordica, Cucurbita, Citrullus, Lagenaria, Luffa,* etc.) possess three stamens of the type mentioned above, but that quite a few genera (*Fevillea, Alsomitra, Zanonia, Hemsleya, Thladiantha, Actinostemma,* etc.) are 5-staminate. All 5 free stamens in this group are monothecal. A few genera like *Anguira, Gurania, Guaraniopsis,* are 2-staminate—both stamens being bithecal. The extreme modification with a single stamen is present in *Cyclanthera.* Occasionally flowers with four stamens (*Lagenaria leucantha* and *Cucumis sativus,* etc.) may develop in normally 3-staminate species.

In *Benincasa* and *Coccinia,* however, the 3 stamens are always bithecal. In *Anisosperma* the 5 stamens are described as being spuriously bithecal, whereas some members of *Telfairia coccinia* (see Naudin) may develop 5 bithecal stamens.

Naudin (1855) considered three as the basic number of stamens in *Cucurbitaceae,* as he regarded the two bithecal stamens with four microsporangia as complete and the odd stamen with one theca (with two microsporangia) as only half complete, thereby accepting the view that the stamens are really two and a half (cf. Saunders' view). According to Naudin, five free stamens each with one theca were formed by splitting of two complete stamens. As mentioned before, Saunders (l.c.) also held this view. Whereas Naudin's plan is principally tri-
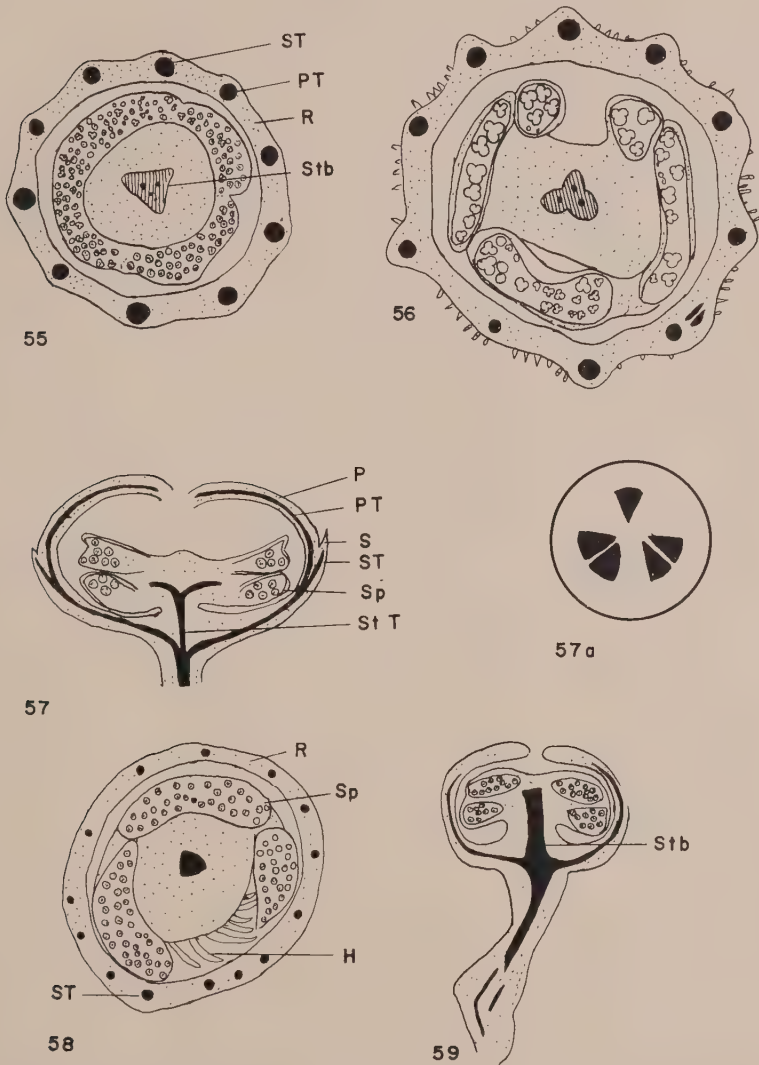
Cyclanthera pedata Schrad., FIG. 55.—Cross section of flower bud showing traces for sepals and petals in receptacle and ring of pollen sacs formed by three anthers; trilobed solid stele in center. × 40. FIG. 56.—Cross section of more mature bud, showing that annular pollen sac is really due to fusion of three stamens with loculus of each arranged in a ring. × 33. FIG. 57.—Longisection of flower bud showing floral traces and sporangia in two rings, one above the other. × 45.
Cyclanthera explodens Naud., FIG. 58. Cross section of flower bud showing a single stamen which is made up of three stamens of unequal size which are not fused; deltoid stele in center. × 40. FIG. 59.—Longisection of a flower bud showing traces for floral members and vestigial stele in staminal region. × 40.

merous, Van Tieghem (1875) constructed a pentamerous vascular ground plan of the stamens of *Cucurbitaceae*. According to this interpretation, ten vascular bundles (traces) supply five stamens (i.e. two bundles per stamen), five bundles being larger and five smaller. Four of the five larger bundles are arranged in two pairs and one remains apart, whereas the two smaller bundles remain between the two pairs of larger bundles; the other two smaller bundles remain in between a larger pair and the larger odd and one smaller between the other larger pair and the larger odd as shown in Fig. 74, i and ii. According to Van Tieghem, the ten smaller bundles disappear ultimately and as a result two stamens with a pair of bundles and one with one bundle develop. Each bundle supplies a theca. Van Tieghem places the stamens opposite the petals. Contrary to Eichler (1875) Van Tieghem assumed that a pair of bundles formed by a small and a large bundle (Fig. 74, iii) supplies a stamen. He also assumed that each bundle supplies a theca but, as the smaller bundles ultimately disappear, five monothecal stamens are formed. Then, the larger bundles lying side by side unite so that ultimately three stamens are formed, two of which are bithecal and the third is monothecal (Fig. 74, iv). After a study of the staminate flowers of *Cucumis sativus* Heimlich (1927) found that the flower is 2½-staminate. Like Naudin he stressed that the two stamens with two thecae are complete and that the one with one theca is half complete. But he admitted that he could not trace the vestigial staminal bundles postulated by Van Tieghem and Eichler. As Heimlich does not believe that vascular bundles alone provide a guide to the morphology of an organ, he suggested that the comparative morphology of the species may provide additional information.

Normally each stamen has a single vascular trace, as shown by Abbe (1940) for *Leitneria floribunda*, Arber (1931) for cruciferous flowers and the *Fumarioideae*, Dawson (1936) for the *Polymoniaceae*, Fischer (1928) for the *Salicaceae*, Grove (1941) for *Agave Lechugilla*, Henderson (1926) for *Plantago*, Jackson (1934) for *Rosa*, Laubengayer (1937) for the *Polygonaceae*, Lindsey (1940) for the *Gentianaceae*, Puri (1947) for the *Passifloraceae*, Quibell (1941) for *Animopsis californica*, Saunders (1936) for the *Cistaceae* and *Malvaceae*, Woodson and Moore (1938) for *Apocynaceae* and others. Arber (1933) has corroborated the conclusion of Hildebrand (1870) and others that the two bundles present in each innermost stamen of *Hypecoum* represent two free stamens of ancestral species. Eames and MacDaniels (1947) state that a single trace is usually the vascular supply of a stamen without regard to size, shape, character of base or period of persistence. They point out however that in some Ranalian families three traces are present and that the three trace condition should be regarded as primitive, as it is exceptionally rare.

Wilson (1937) in discussing the phylogeny of the stamen called attention to the fact that in certain *Parietales* and *Malvales* of Engler the vascular supply of a number of stamens arises by the division of a single strong bundle which he terms 'the stamen fascicle trace.' In discussing the telome theory he (1942) states that the anther is a synangium of four sporangia and that this synangium together with the filament and connective has arisen from a dichotomous branch

Thladiantha dubia Bunge, FIG. 60.—Cross section of pedicel showing vascular bundles centrally disposed, surrounded by ring of pericycle. × 30. FIG. 61.—Cross section of flower bud showing five free staminal traces (in 2+2+1 arrangement) on one side of receptacle. × 28. FIG. 62. Same, at a higher level, showing five free stamens, with unequal sporangia and undulate wall; paired stamens shown by arrows. × 30. FIG. 62a.—Cross section of theca showing two sporangia. × 50. FIG. 63.—Traces of two stamens meet at receptacle and then diverge again.

system with terminal sporangia. He supports the view held by Thomas (1931–1933) that the vascularization of the three trace stamens has been derived by reduction and fusion of a dichotomous branch system.

My study of the stamens of 14 species representing ten genera shows that both 3-staminate and 5-staminate flowers are alike in showing five bundles given off from the vascular system of the receptacle. The number of stamens in this family is definitely five. They are essentially opposite the sepals but the axis may be opposite a sepal or a petal (e.g., *Lagenaria*, *Cucurbita*). Four of the five stamens may unite in pairs, while one remains free. The position of the stamens with reference to the axis changes in different genera (cf. Fig. 64–71). The reduction in number of stamens from 5 to 4, 3, 2 or 1 can be traced in different members. In the flowers of 3-staminate species (*Trichosanthes*, *Momordica*, *Lagenaria*, *Cucurbita*, etc.) five staminal traces arising from the inner side of receptacular stele pass through the inner wall of the receptacle in a $2+2+1$ arrangement. Although their basic angular distance is 72° apart, they assume this arrangment at a higher level (cf. Fig. 52). Two bundles of a bithecal stamen ultimately unite at a higher level either at the receptacle (*Trichosanthes anguina*) or at the base of the filament (*Benincasa hispida*) or in the filament, but usually they unite in the connective (*Cucurbita*, *Coccinia*, etc.). In *Lagenaria* (Fig. 8) a pair of traces wide apart from one another, can be traced to higher level in the connective without fusion.

In all species the pair of traces of the stamens branches at the connective before and after fusion and these branches supply the convoluted thecae. The traces are practically independent in their manner of development and branching. In *Trichosanthes anguina* the fused traces bifurcate at the upper part of the connective (Fig. 20). In *Bryonia dioica* the traces remain united in the filament and separate again at the bilobed anther. In *Cucurbita pepo* the union of two bundles in the formation of a bithecal stamen can be seen even with the naked eye. By carefully removing the trilobed glandular pistillodium the fusion at the connective (Fig. 52) of the two bundles of a bithecal stamen arising at a distance apart can be demonstrated. As the filaments are very minute in many cases, it is often very difficult to determine whether the stamens are united at the base or apex of the filament, but their union at the connective is often clear. In some cases (*Bryonia*, *Trichosanthes*, etc.) the fusion of the traces takes place at the receptacle. Here their (traces) larger size and lobed nature indicate their compound structure, and they can be easily distinguished from the smaller trace of the odd stamen. It has been clearly seen that each of the traces forms the vascular supply of a theca. In bithecal stamens each trace supplies a theca more or less independently, even though they fuse at the connective. The fusion is a purely mechanical one, as ontogenetically they are distinct individuals.

When all the thecae are bisporangiate, a bithecal stamen has four microsporangia and a monothecal stamen has two microsporangia. As a bithecal stamen thus appears to have been formed by fusion of two monothecal stamens, it is morphologically a compound or double stamen and not a single one. On the basis of his external morphological examination of a few genera like *Fevillea*, *Anisosperma*, *Actino-*

stema, Zanonia, Thladiantha, Sicydium, and *Bryonia,* Pax (1890) suggested that the so-called bithecal stamens are the result of fusion of two monothecal stamens. The monothecal odd stamen is complete in itself. In this case one of the two thecae (loculi) of a normal anther has been suppressed.

Evidence based on examination of a number of species and genera shows that bithecal stamens result from the fusion of two monothecal stamens. Naudin's view, supported partly by Saunders, that the
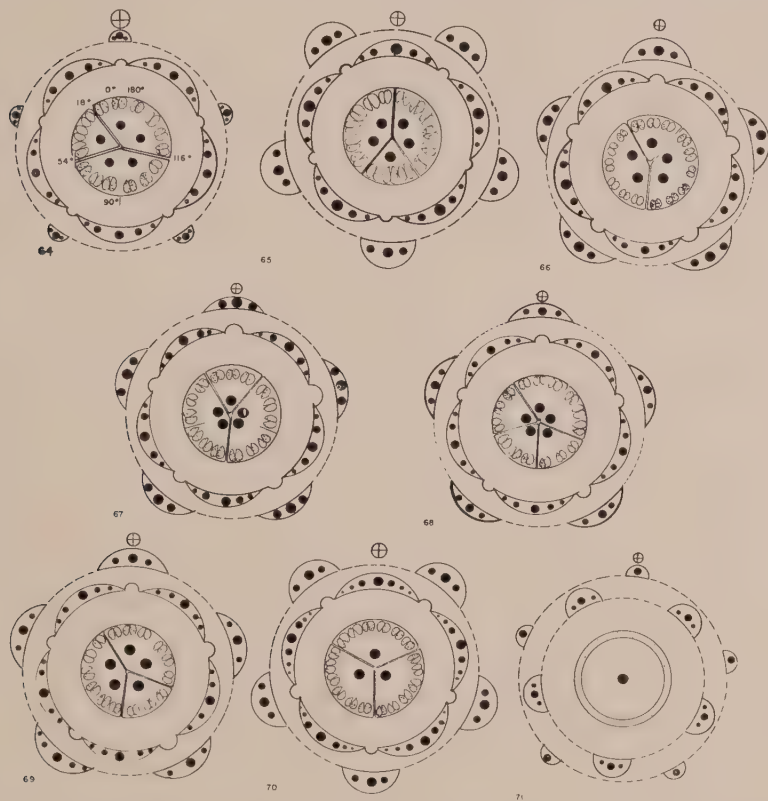
Vascular floral diagrams, FIG. 64.—*Trichosanthes anguina;* FIG. 65.—*Lagenaria leucantha* and *Cucurbita pepo;* FIG. 66.—*Momordica charantia;* FIG. 67.—*Luffa cylindrica* (with 3 stamens); FIG. 68.—*Luffa cylindrica* (with 5 stamens); FIG. 69.—*Cucumis melo* and *Cucumis sativus;* FIG. 70.—*Benincase hispida;* FIG. 71.—*Cyclanthera pedata.*

five free monothecal stamens were derived by splitting of two bithecal stamens, is very difficult to understand, as in all cases (cf. *Lagenaria, Cucurbita*) I find no trace of splitting of bundles but clear evidence of their union. In *Lagenaria* and *Cucurbita* the traces of the stamens are round in shape and separated by a broad band of ground tissue. These two genera offer excellent examples of how staminal traces arise

at different points in the receptacle, gradually approach, and enter a
filament, a behavior that cannot easily be explained by splitting.
In *Luffa cylindrica* the stamens fluctuate between 3 and 5 in the same
plant or even in the same inflorescence. When five stamens are present,
each is separately supplied with a single vascular strand and the
flowers with three stamens show an arrangement of traces like *Lagenaria*,
Cucurbita, etc. However, the monothecal stamen with two sporangia
retains its original bithecal habit in a good number of cases among the
three staminate flowers (cf. Fig. 41). The genus *Anisosperma* with
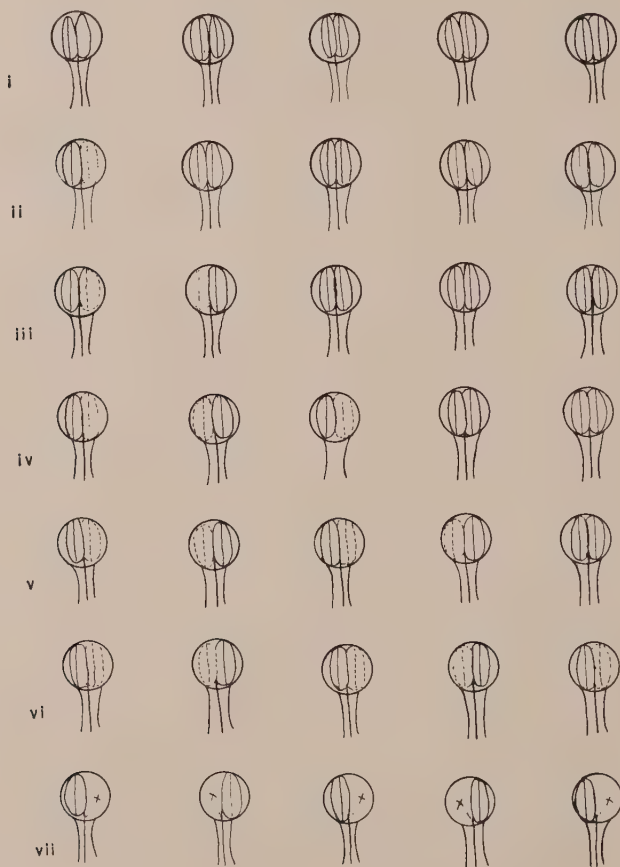
72

Ontogenetic development of stamens. FIG. 72.—(i) all perfect stamens, this
type is approached by *Anisosperma* with 5 free spuriously bilocular stamens: (ii)
one theca weaker, (iii) two thecae weaker, one on right and one on left, (iv) three
thecae weaker, (v) four thecae weaker, (vi) five thecae, one theca in each stamen,
weaker, (ii-vi, examples unknown); (vii) five monothecal stamens, one theca
suppressed in each stamen (*Fevillea, Alsomitra, Gerardanthus, Hemsleya, Sioalmatra,
Zanonia, Actiostemma, Gomphogyne*, etc., sometimes *Luffa cylindrica.*

five free stamens develops bithecal stamens, whereas in some members of *Telfairia* (cf. Naudin) and rarely in *Coccinia cordifolia* (cf. Chakravarty and Sen Gupta) five bithecal stamens have been observed.

In *Thladiantha dubia* (Figs. 61–63) two pairs of five stamens arise in close proximity on the receptacle. Their traces are seen to approach each other and touch when followed through the receptacular tissue, but lower down these traces diverge again.

It is probable then that *Thladiantha*, *Neoluffa*, *Fevillea*, etc. with five free stamens, four of which form adjacent pairs, represent a stage
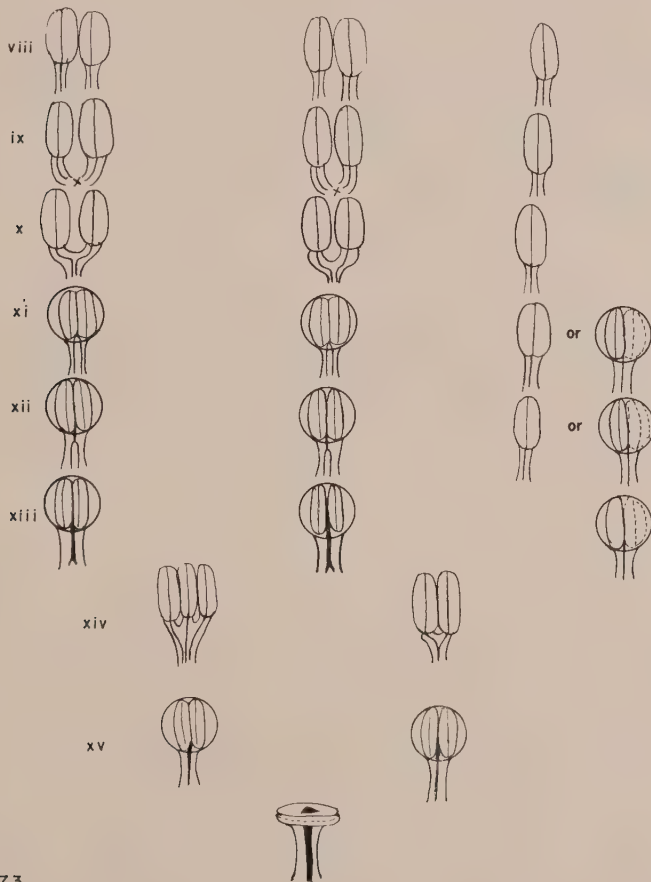
FIG. 73, (viii) *Thladiantha*—four in two groups, one apart, all free; (ix) *Neoluffa*—two pairs arise from a common base: (x) *Sicydium*—two pairs united by the filaments below; (xi) *Lagenaria*, *Cucurbita*, etc., filaments fused, but traces of original stamens remain seperated; (xii) *Cucumis*, *Coccinia*—filaments free below and fused above; (xiii) *Benincasa*—filaments united all through: notice reversion to bithecal character of the odd stamen in xi, xii, xiii; (xiv) *Luffa tuberosa* (sometimes); (xv) *Anguira*, *Guraniopsis*, *Gurania*, etc., (xvi) *Cyclanthera*. (All figures semi-diagrammatic).

in the production of a three staminate flower from a more primitive five staminate form.

Variation in three staminate flowers has occasionally been observed, as in *Lagenaria leucantha* (stamens 4, 1 bithecal, 3 monothecal), *Coccinia cordifolia* (stamens 3, all bithecal), and *Cucumis sativus* (stamens 4, 2 bithecal, 2 monothecal). In *Benincasa hispida* and in *Coccinia cordifolia* all stamens are bithecal as occasionally found in *Cucurbita*, *Lagenaria*, etc. It has been pointed out that in cases of three bithecal stamens one (the so-called odd one) contains a single trace and the other two possess two traces each.
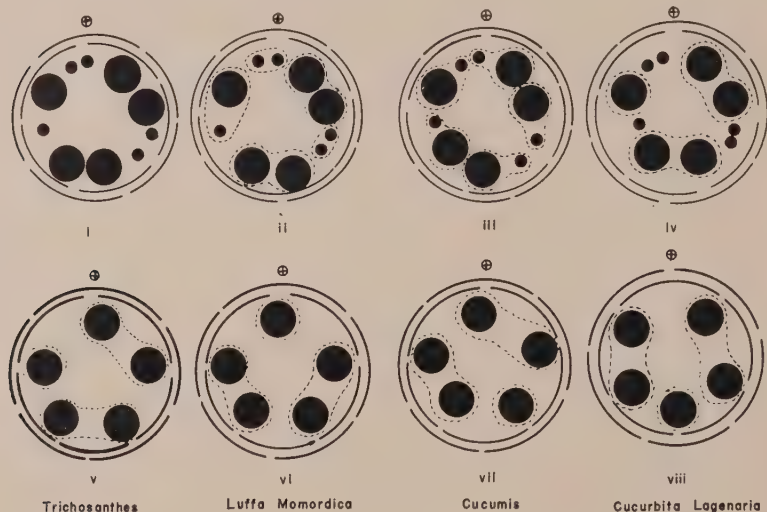
Fig. 74. Vascular ground plan of the stamens. (i) and (ii)—Van Tieghem's conception; (iii) and (iv)—Eichler's conception; (v-viii)—author's findings; (v) —*Trichosanthes anguina*, (vi)—*Momordica charantia* and *Luffa cylindrica*; (vii)— *Cucumis sativus* and *Cucumis melo*; (viii)—*Lagenaria leucantha* and *Cucurbita pepo*.

The facts presented above suggest that the modern flowers of the *Cucurbitaceae* have evolved from a stock which had five free stamens each with four microsporangia in two thecae. Subsequent changes brought about a reduction resulting in an anther with one theca. A single trace supplied each stamen, forked (or branched) at the summit, and each of these branches supplied a theca (Fig. 72). This arrangement is usual in other flowering plants. In the next stage a fork (a branch) with a theca on the right of one of the stamens became weaker. Following this tendency of reduction a similar weakness of the fork and the theca on the left of the adjacent stamen may be conceived. This process perhaps continues for long periods until we arrive at a stage when of the five complete stamens a theca on the right and a theca on the left alternately become weaker. These weaker thecae have been illustrated in dotted lines (Fig. 72). At further stages

of evolution we can assume the gradual reduction of the weaker thecae till we arrive at a stage (Fig. 72, vii) when a theca from each complete stamen has ceased to develop. This arrangement is found in almost all genera (*Fevillea, Gerardanthus, Actinostemma, Zanonia, Alsomitra, Thladiantha,* etc.) with five stamens. It can be assumed that the stamen on the extreme right undergoes reduction of a theca last or that it retains the tendency of developing a bithecal stamen or that it fluctuates between a monothecal and bithecal condition.

Assuming these stages of evolution greatly facilitates interpretation of the stamens of living members of the *Cucurbitaceae.* Starting from the last series of stamens (Fig. 72, vii) with one theca (represented by a number of genera) we find that two lateral ones approach closer to one another (*Thladiantha, Fevillea,* etc.), or even arise from a common point (*Neoluffa,* vide Chakravarty). In the next stage, found in *Sicydium,* the filaments are united below. In *Bryonia* the filaments are united throughout the whole length, while the anthers remain
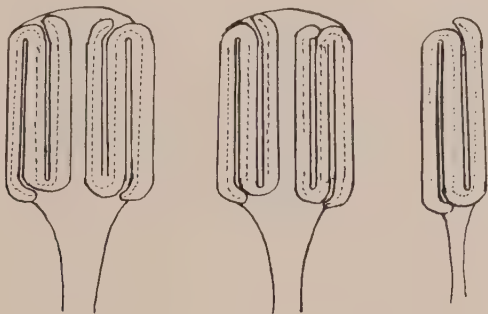
75

FIG. 75. Usual three staminate flowers of *Cucurbitaceae,* two bithecal and one monothecal, each theca thrice folded (semidiagrammatic).

free. The following stage is represented by a number of genera in which the filaments are united throughout the whole length but with two traces of original stamens still separated (cf. *Cucurbita, Lagenaria*— Fig. 72, x, xi). In other genera the fusion of the traces takes place almost at the base of the filament (*Cucumis, Coccinia,* etc.) and, in the extreme case, the traces are united in the filament at the very base (*Benincasa*) or even in the receptacle (*Trichosanthes anguina*).

In *Luffa tuberosa* occasionally two stamens, one with three thecae and one with two thecae, are seen (Fig. 73, xiv), but usually one is monothecal and two are bithecal. In *Anguira, Gurania,* and *Guraniopsis* two stamens each with two thecae are found (Fig. 73, xv). The extreme modification of stamens fused into a single one is found in *Cyclanthera.* Here the anther is annular with two pollen chambers disposed one above the other (Fig. 72, xvi). As described above, this stamen is formed by union of three stamens (Figs. 55, 56, 58). It is interesting to note that the thecae of five free staminate genera are all

erect or slightly curved while they are convoluted in three united
(2+2+1) staminate genera. With the reduction of the number of
stamens, the pollen area is apparently increased by transformation of
the pollen sac into a long convoluted form.

The pentamerous vascular floral ground plan illustrated by Van
Tieghem (Fig. 74, i, ii) and Eichler (Fig. 74, iii, iv) approaches closely
the vascular construction of the stamen but their supposition of smaller
traces along with larger traces is purely hypothetical. Van Tieghem's
plan of five stamens as given in Fig. 74 (ii) is theoretical. Eichler's
(Fig. 74, iii, iv) plan is more logical although the smaller traces associated
with a larger trace in two compound stamens have not been found in
any members of the *Cucurbitaceae*. No vestigial trace occurs in the
stamens. Heimlich (*l.c.*) also failed to find such a trace in *Cucumis
sativus*. It is plausible and logical to assume that the single staminal
trace forks dichotomously in the formation of a theca as suggested by
Wilson (1937).

The flowers of the *Cucurbitaceae* are definitely pentamerous. The
three stamens possess 2+2+1 traces, each trace representing the
position of an original stamen (Fig. 74, v-viii). Of these traces 4 unite
in 2 pairs and the odd one remains free. The stamens basically are
sepal opposite in all, e.g., *Trichosanthes anguina*, *Momordica charantia*,
Luffa cylindrica, *Cucumis sativus*, *Cucumis melo*, *Lagenaria leucantha*,
and *Cucurbita pepo*; but the axis may be sepal opposite (Fig. 74, v) or
petal opposite (Fig. 74, viii). The position of the odd stamen and the
compound stamens with relation to the axis is not fixed in all genera,
as they may be the same in a few genera and may change from genus
to genus (cf. Figs. 66–71).

The unusual formation of stamens in some genera and species has
been studied with particular attention. In *Benincasa hispida* (Fig.
67), and occasionally in *Cucurbita pepo*, *Lagenaria leucantha*, *Coccinia
cordifolia*, three bithecal stamens are present. On examination of
these stamens, particularly those of *Coccinia cordifolia*, it is found that
two of these stamens are compound in nature having fused traces
(Figs. 38, 39, 40) and that the other is a complete one having a single
trace. This bithecal third stamen is a case in which the original
habit is retained. This stamen has either one or two thecae (cf. Fig.
73, xii). But in *Benincasa* this odd stamen usually develops two
thecae. In all these cases the dimensions of the filaments of three
stamens vary. Two filaments are always thicker than is the third.
In four staminate *Lagenaria*, one is bithecal with two traces and the
other three have a trace in each. Of the three monothecal stamens
two have not united in this case (Fig. 14). In the four staminate
Cucumis sativus (Fig. 36) we find two bithecal and two monothecal
stamens. In this case one of the bithecal stamens has two traces and
the other has only one. Of the two bithecal stamens, though
homologous to one another, one (with two traces) is morphologically a
compound stamen and the other is a complete (with two loculi and
one trace) stamen. The latter (which is homologous to an odd stamen
but analogous to a compound stamen) is a case in which the original
habit has been retained. The species mentioned above have been
examined in the field and in the laboratory, where illustrations were
drawn under microprojection.

The bundles of the pedicel are bicollateral as are most of the bundles of the stamens. But bundles of the calyx and corolla are mostly collateral as the innermost phloem tissue ceases to develop in these cases. The smaller traces of the calyx and corolla and the branches of the staminal traces are often concentric (amphicribral) or the xylem and phloem elements are not symmetrically arranged. However in most cases the larger traces of the stamens are bicollateral, although higher up the inner phloem decreases in bulk and ultimately ceases to exist making the traces collateral. The vein ends are often made up of a few protoxylem elements, especially those with spiral and seldom with annular thickenings. De Bary (1884) found concentric bundles in the leaves of certain Cucurbitaceae (see Holroyd 1924).

CONCLUSION

In the basis of the evidence presented, I concluded that the basic number of stamens in the *Cucurbitaceae* is five with one trace in each. Each stamen of the flowers of five-staminate genera, though monothecal individually, should not be considered as a half stamen but should be regarded as a complete stamen that has lost one theca. The stamens of the flowers of the three staminate genera are derived from five independent monothecal stamens. Through fusion of a pair of adjacent monothecal stamens two bithecal stamens (with 4 sporangia) are formed, while the other (odd) stamen takes no part in the fusion process and remains apart. The bithecal stamens should therefore be regarded as compound stamens rather than complete stamens as postulated by some, whereas the odd stamen should be interpreted as a simple stamen (with 2 sporangia), because the suppression of a theca did not materially change its structure. The occasional appearance of two thecae in this stamen reveals its original habit.

SUMMARY

Male flowers of fourteen species belonging to ten genera (*Trichosanthes, Lagenaria, Momordica, Luffa, Bryonia, Cucumis, Benincasa, Coccinia, Cucurbita*, and *Cyclanthera*) have been studied with special reference to the morphology and evolution of the stamens.

Pedicels in almost all these cases have bicollateral bundles the number of which is not constant because they branch throughout their course. At the base of the receptacle, the structure formed by cohesion and adnation of the calyx and the corolla, the vascular bundles coalesce (except in *Trichosanthes, Luffa, Momordica*) and form a radiating siphonostele. Fifteen traces for the sepals (three for each sepal) and five traces for the petals (one for each petal) branch from the outer region of the stele and run along the outer surface of the receptacle. The petal traces arise at a slightly higher level than the sepal traces and alternate with a group of three sepal traces. The petal lateral traces are formed by a branching of the petal main at a higher level in the receptacle. In *Trichosanthes anguina, Luffa cylindrica, Momordica charantia*, and *Coccinia cordifolia* the vascular bundles do not really coalesce at the receptacle but form a central ring like a dissected siphonostele and the traces radiate in the same manner as indicated above. In *Cyclanthera pedata* and *C. explodens* ten traces start from

the solid vascular cylinder formed at the base of the receptacle. Alternately one trace goes to each sepal and one to each petal.

Toward the inner side of the siphonostele, or dissected siphonostele as the case may be, and at a slightly higher level five larger traces for stamens branch out and pass through the inner surface of the receptacle (bending at the region of the pistillodium) in $2+2+1$ arrangement. A pair of closer traces of the bithecal stamens fuses either at the receptacle or at the filament but mostly in the connective where they branch and supply the convoluted thecae. The trace for the odd stamen passes alone into a filament. The fusion of the pairs of traces of the two bithecal stamens takes place at different levels. The filaments too of these stamens detach themselves from the receptacle at different levels for the purpose of better accommodation of space. A bithecal stamen formed by the fusion of two monothecal stamens has two traces and therefore is morphologically a compound stamen. Hence in the three staminate flowers, two are compound and one is simple.

The suppression of a theca without fundamentally changing the construction of the stamen has been ontogenetically ascertained. Critical examination of the simple stamen of *Cyclanthera* (*C. explodens* and *C. pedata*) revealed that it is produced by fusion of three stamens. A morphological explanation of flowers with 3 bithecal stamens (*Benincasa hispida, Coccinia cordifolia*), flowers with four stamens one of which is bithecal and the rest monothecal (*Lagenaria vulgaris*), and flowers with four stamens with two bithecal and two monothecal anthers (*Cucumis sativus*) was attempted from an ontogenetic viewpoint. The available evidence proves that the flower of Cucurbitaceae is pentamerous, that the basic number of stamens is five, and that the three stamens usually present result from fusion of two lateral stamens.

Various shorter and weaker traces develop from the inner side of the stele (like the traces of androecium)at a slightly higher level than that of the stamens and pass into the trilobed glandular pistillodium. These traces are usually arranged in a circle on the outer wall of the pistillodium but quite a few are also found scattered within, where they often coalesce.

In conclusion I acknowledge my grateful thanks to Dr. H. Hamshaw Thomas, Sc.D., F.R.S., under whose kind supervision the work has been completed. Thanks are also due to the Director of the University Botanic Garden, Cambridge, for raising the plants under tropical conditions in the experimental house of the garden. To the Government of Bengal I am grateful for extending my study leave for this problem.

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Orchidaceae Neotropicales V.   Generis Aganisiae Synopsis

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Recent field work—especially in the northwestern Amazonia of Brazil and Colombia and the headwaters of the Orinoco in Venezuela—has made available for study interesting and ample material of several species of *Aganisia* which have hitherto been rather sparsely represented in our herbaria.   In view of this new material, it would seem to be worthwhile to present a short synopsis of the orchidaceous genus *Aganisia* (including *Acacallis*) as a contribution towards a fuller understanding of that difficult complex of genera of the *Zygopetalinae* which are most closely related to *Aganisia*.

It is a pleasure for me to express my appreication to Dr. Kurt Rechinger, director, and Dr. Kurt Fitz, teachnical assistant, of the Botanische Abteilung of the Naturhistorisches Museum in Vienna for the loan of 19 sheets of *Aganisia* (comprising specimens, analytical drawings, letters, and descriptions) from the Reichenbach Herbarium. I have also to acknowledge the kind cooperation of the authorities of the following herbaria for the loan of material in their care: Royal Botanic Gardens, Kew; Imperial College of Tropical Agriculture, Trinidad; New York Botanical Garden; Chicago Natural History Museum; and Smithsonian Institution, Washington, D. C.   The present study has been based upon the collections in these herbaria, in addition to those preserved in the Gray Herbarium and the Orchid Herbarium of Oakes Ames at Harvard University.

It is not within the scope of this paper to review the relationships of the genera of the *Zygopetalinae*, especially *Aganisia*, *Koellensteinia*, *Otostylis*, *Paradisanthus* and *Wareella*.   *Aganisia* (including *Acacallis*) may be distinguished at once, even vegetatively, from *Koellensteinia*, *Otostylis*, and *Paradisanthus*, since it has a greatly elongated rhizome with distant pseudobulbs and a scandent, epiphytic habit, as contrasted to a short rhizome with aggregated pseudobulbs and a terrestrial habit.   *Wareella* is unique in this group of genera in having no evident pseudobulbs.

My research leads me to the conclusion that the two generic concepts which have been called *Aganisia* and *Acacallis* are not sufficiently distinct to warrant continued maintenance as separate entities. Botanists who have worked on the problem are at variance. Bentham (Bentham, G. in Journ. Linn. Soc. Bot. 18 (1881) 30; Bentham, G, and Hooker, J. D. "Genera Plantarum" 3 (1883) 544) maintained *Aganisia* and *Acacallis* as separate concepts.   Schlechter (Schlechter, R.: "Die Gattung *Aganisia* Ldl. und ihre Verwandten" in Orchis 12 (1918) 24–42) argued for keeping *Aganisia* and *Acacallis* as distinct. Hoehne (Hoehne, F. C. "Flora Brasilica" 12, pt. 7 (1953) 155 ff.) followed Schlechter in his disposition of these two concepts.   As early as 1888, however, Pfitzer (Pfitzer, E. "Orchidaceae" in Engler-Prantl: "Die natürlichen Pflanzenfamilien" 2, Abt. 6 (1888) 164, 166) united the two.   In January 1944, Mr. Charles Schweinfurth, in a

handwritten annotation in the Orchid Herbarium of Oakes Ames, stated: "I do not agree that *Acacallis* is specifically distinct from *Aganisia*"; and, in his forthcoming "Orchids of Peru", he continues to treat *Acacallis* as synonymous with *Aganisia*.

The characters which have been employed to separate *Aganisia* from *Acacallis* appertain primarily to the structure of the callus of the lip and to the presence or absence of a distinct claw.   Study of the ampler material now available indicates that there is some variability in the amount and form of verrucosity and lobing of the callus.   Furthermore, there is appreciable variability in the distinctness and length of the claw in flowers from different plants and of its degree of fusion with the column base.   I cannot find either in the literature or in the material which I have studied any additional differences by which the two concepts may be distinguished.   In view of the relatively minor nature of these characters and the obvious variability in them, I concur with Pfitzer and Schweinfurth in reducing *Acacallis* to synonymy under *Aganisia*.

Schlechter (loc. cit.) and Hoehne (loc. cit.) have outlined the historical development of our knowledge of *Aganisia*, but it may be worthwhile to repeat it briefly here, especially since my point of view differs taxonomically.

Aganisia was described in 1839 by Lindley for a species collected in British Guiana which he named *A. pulchella*.   One year later (in Bot. Reg. 25 (1840) t. 32), an illustration was published.   The material collected in British Guiana flowered in England.   Lindley wrote that if "its column were produced into a foot, and the lower sepals unequal at the base, it would be a *Maxillaria* . . .".

Thirteen years later, Lindley proposed the genus *Acacallis*, describing *Acacallis cyanea*, based on material gathered by Spruce in the basin of the Rio Negro of the Brazilian Amazon, stating that it had relationships with *Huntleya*, *Warrea* and *Paradisanthus* but not mentioning its closeness to *Aganisia*.   In 1869, Reichenbach recognized it as a species of *Aganisia* and made the indicated transfer.   In the same year, he described as *Aganisia lepida* material collected on the Rio Negro in Brazil.

A third species of *Aganisia* was proposed in 1874 by Reichenbach when he described *A. fimbriata* on the basis of material collected in British Guiana and brought to flower in England.

Two years later, Reichenbach described *Aganisia coerulea* from material collected somewhere in Brazil and brought to flower in the Hamburg Botanical Garden.

Shortly thereafter, in 1878, he proposed *Aganisia Oliveriana* for a Brazilian plant that flowered also in the Hamburg Botanical Garden, indicating that its affinities lay with *A. fimbriata*.   A drawing of *Aganisia Oliveriana* appeared in 1883.

Bentham (Bentham, G. in Journ. Linn. Soc. London, Bot. 18 (1881) 320) suggested that *Koellensteinia* should be united with *Aganisia*, and this was carried out by Nicholson (Nicholson, Dictionary of Gardening, 1 (1885) 35).   The result was an additional binomial under *Aganisia* (*A. ionoptera*).

In 1885, N. E. Brown described *Aganisia tricolor* from plants which

had been introduced from the Amazonian regions, presumably of Brazil. Brown pointed out that it differed from *Aganisia cyanea* primarily in color.

Ridley proposed *Aganisia alba* in 1886 from material collected in British Guiana by the Roraima Expedition.

Schlechter created a monotypic genus—*Kochiophyton negrense*—in 1906, for a collection from the Rio Negro of Brazil, and several years later Hoehne added a second species—*K. coeruleus*. Schlechter himself later reduced both species to synonymy under *Aganisia cyanea*.

Another binomial—*Aganisia boliviensis*—was published by Rolfe in 1907 for a plant from Bolivia which he himself indicated to be very close to "*Aganisia ionoptera* Nichols.".

A final binomial under *Aganisia* was proposed by Schlechter in 1925, when he described *A. brachypoda* from a collection made in the upper Rio Negro basin of Brazil.

AGANISIA Lindley in Bot. Reg. 25 (1839) Misc. 65, p. 45; *ibid.* 26 (1840) t. 32; Endlicher Gen. Plant., Suppl. 1 (1840) 1363; Beer Prakt. Stud. Fam. Orch. (1854) 187; Duchartre Man. Gen. Plant. 4 (1857) 474; Reichenbach fil. in Walpers Ann. Bot. 6 (1861) 504; Beitr. zur Orchideenk. (1869) 9; DuBuysson L'Orchid. (1878) 180; Bentham & Hooker fil. Gen. Plant. 3 (1883) 544; N. E. Brown in Lindenia 1 (1885) 95; Pfitzer in Engler & Prantl Die Natürl. Pflanzenfam. 2, Abteil. 6 (1888) 166; Stein, Orchideenb. (1892) 66; in L'Orchidoph. 2 (1892) 84; Bois Orch. (1893) 128; Kerchove Livre des Orch. (1894) 267; Williams Orch.-Grow. Man., ed. 7 (1894) 93; Schlechter Die Orchideen (1915) 418; in Orchis 12 (1918) 10; Hoehne Iconogr. Orch. Brasil. (1949) 221; Flora Brasilica 12, 7 (1935) 155; Ospina Orquid. Colomb. (1958) 179, 180.

Acacallis Lindley Fol. Orch. (1853) *Acacallis*; Reichenbach fil. in Walpers Ann. Bot. 6 (1861) 505; Bentham in Journ. Linn. Soc. London, Bot 18 (1881) 320; Bentham & Hooker fil. Gen. Plant. 3 (1883) 544; L'Orchidoph. (1892) 84; Veitch Man. Orch. Plants 9 (1893) 69; Cogniaux in Journ. des Orch. 4 (1894) 320; Linden Orch. Exot. (1894) 563; Cogniaux in Martius Fl. Bras. 3, pt. 5 (1902) 524; Schlechter Die Orchideen (1915) 418; in Orchis 12 (1918) 11; Hoehne Iconogr. Orch. Brasil. (1949) 221; Flora Brasilica 12, 7 (1953) 160; A. D. Hawkes in Orch. Journ. 2 (1953) 98.

Kochiophyton Schlechter ex Cogniaux in Martius Fl. Bras. 3, pt. 6 (1906) 574, t. 119; in Koch-Grünberg Zwei Jahre unter den Indianern 2 (1910) 364.

Epiphytic or terrestrial herbs, often creeping and almost vine-like. Pseudobulbs very small, cylindrical to fusiform, usually completely hidden by long, sheathing bracts, usually 1-foliate (rarely 2- or 3-foliate). Leaves petiolate, plicate, papyraceous. Inflorescence a lateral, lax, short-pedunculate, erect or arcuate, several- to 10-flowered raceme. Flowers usually large and showy, short-pedicellate. Bracts small. Sepals free, spreading. Petals subsimilar to sepals. Lip subsessile to long-clawed, 3-lobed or simple; lateral lobes (when present) usually small; mid-lobe more or less concave, spreading, large, often emarginate or sublobulate; disk prominently cristate. Column short,

erect, with or without foot, conspicuously winged and 2-auriculate at apex. Anther terminal, opercular, incumbent, 1-celled. Pollinia 4, waxy, complanate-obovoid.

Aganisia: from the Greek, signifying "pleasing to the sight".

A genus of three species known from northern South America and Trinidad.

Key to the Species of Aganisia

I.   Margins of mid-lobe of lip entire or subentire.   Basal lobes of lip relatively conspicuous, broadly rounded.   Flowers white or yellowish with a few red or purple spots at base of lip..........................3.   *Aganisia pulchella*

Ia. Margins of mid-lobe of lip not entire.   Basal lobes of lip very small, obtuse or subacute.   Flowers predominantly pale blue or brownish blue.

    II.   Lip long-clawed, 25–30 mm. long (including claw).   Mid-lobe of lip irregularly and minutely crenulate-dentate.   Callus of lip irregularly verrucose, 8 mm. high............................1.   *Aganisia cyanea*

    IIa. Lip short-clawed, up to 14 mm. long (including claw).   Mid-lobe of lip fimbriate.   Callus of lip triangular-lobulate, 2–3 mm. high......
                          2.   *Aganisia fimbriata*

    1.   **Aganisia cyanea** (Lindl.) Reichenbach fil. in Beitr. zur Orchideenk. (1869) 13, t. 4; Linden & Rodigas in Lindenia 3 (1887) 31, t. 110; Veitch, Man. Orch. Plants 9 (1893) 68; Williams, Orch.-Grow. Man. ed. 7 (1894) 94; Ospina Orquid. Colomb. (1958) 179, 180, t. 8.

Acacallis cyanea Lindley Fol. Orch. (1853) *Acacallis*; Reichenbach fil. in Walpers Ann. Bot. 6 (1861) 505; Veitch, Man. Orch. Plants 2 (1885) 70; Cogniaux in Martius Fl. Bras. 3, pt. 5 (1902) 524; Rolfe in Orch. Rev. (1907) 40; Curtis' Bot. Mag. s. 4, 12 (1916) t. 8678; Gard. Chron. 60 (1916) sub "Book Notices"; Hoehne in "Com. Lin. Tel. Estr. Matto-Grosso Amazonas" Ann. 5, Bot. Parte 9 (1916) 33; Schlechter in Orchis 12 (1918) 12, t. 1, figs. 9–10; Orch. Rev. 36 (1928) 281; Garnett in Orch. Rev. 37 (1929) 45, 47; *ibid,* 38 (1930) 205, 219; *ibid,* 45 (1937) 174; Hoehne in Arch. Inst. Biol. 8 (1937) 282; Am. Orch. Soc. Bull. 6 (1937) 20. t.; Orch. Rev. 46 (1938) 113; Hoehne "Inconogr. Orch. do Brasil" (1949) 86, 87, 94, 221, t. 225; Hoehne "Ind. Bibl. e Num. Pl. Col. Com. Rondon" (1951) 165; Orch. Rev. 59 (1951) 144; Orch Journ. 2 (1953) F6, t. 38; Fl. Brasilica 12, pt. 7 (1953) 161, t. 73; Am. Orch. Soc. Bull. 26 (1957) 101.

Aganisia tricolor N. E. Brown in Lindenia 1 (1885) 95, t. 45; Williams, Orch.-Grow. Man., ed. 7 (1894) 95; E. S. Rand (ex Am. Gard.) in Orquídea 8 (1945) 66.

Aganisia coerulea Reichenbach fil. in Gard. Chron., n.s., 25 (1886) 720; Warner & Williams, Orch. Alb. 8 (1889) 374.

Kochiophyton negrense Schlechter ex Cogniaux in Martius Fl. Bras. 3, pt. 6 (1906) 574; Schlechter in Koch-Grünberg "Zwei Jahre unter den Indianern" 2 (1910) 365, t.p. 366; Schlechter in Orchis 12 (1918) 13.

Kochiophyton coeruleus Hoehne in Com. Lin. Flor. Matto-Grosso, Annexo 5, pt. 1 (1910) 49, t. 39.

Acacallis Hoehnei Schlechter in Orchis 12 (1918) 14.

Epiphytic herb.   Rhizome repent, up to 5 mm. in diameter, sometimes up to 4–5 m. long, covered with distichous, appressed sheaths, especially in young state. Pseudobulbs distant, 3–20 cm. apart, usually fusiform, slightly beaked, 3–7 cm. long, covered (initially at least) by long, papery, accrescent sheathing bracts, usually 1-foliate. Leaf firmly membranaceous, elliptic to oblanceolate, short-acuminate, basally cuneate, 10–30 cm. long, 4–10.5 cm. wide, with 7 prominent veins beneath; petiole rather stout, channelled, up to 6 cm. long. Inflorescence long-pedunculate, usually about as long as the leaf, nodding, laxly 2 to 10-flowered.   Bracts ovate-triangular, 4–5 mm.

long. Flowers large, conspicuous, pale blue with copper-purplish or wine-colored lip and whitish, brownish or brown-purple column, 3–4.5 cm. in diameter (rarely larger). Sepals and petals spreading, ovate to subrotund, usually apiculate, basally cuneate, 3 cm. long, 2 cm. wide; petals often undulate, commonly slightly smaller than sepals but sometimes wider. Lip long and narrowly clawed, 3-lobed, 25–30 mm. long (including claw); lateral lobes erect-spreading, minute, triangular-dentiform, subacute, 1.5–2 mm. long; mid-lobe thin-membranaceous, pinkish blue to rose-purple, somewhat concave, flabellate, basal margins entire, lateral margin irregularly and minutely crenate-dentate, sometimes apparently lightly emarginate apically, about 15–17 mm. long, 22–27 mm. wide; callus yellowish, fleshy, cristate, irregularly verrucose, 7.5–8 mm. high. Column brownish or white, erect, slightly arcuate, slender, triquetrous or semiterete, up to 17 mm. long, above with 2 membranaceous, suborbicular, reddish or purplish, auricular wings.

BRAZIL: Estado do Amazonas, Rio Negro, "Barra [Manáos]. On trees by forest streams". July 1851, *R. Spruce 1790* (Hb. Kew; Hb. Benth.).—Estado do Amazonas, Rio Uaupés, "Secus cataractam Panuré [Ipanoré]. January 1853. *R. Spruce 1790* (Hb. Kew; Hb. Benth.; Hb. Hook.).—Estado do Amazonas, Rio Negro, near Lake Maracapurí. No date. *E. Morris s.n.* (Hb. Reichenb. 40591, 30476.)—Estado do Amazonas, Rio Negro, Uaupés (São Gabriel) and vicinity. "Epiphyte. Flowers pale blue." October 15–19, 1947. *R. E. Schultes & F. López 8943* (Hb. Ames 67534.)—Estado do Amazonas, Rio Uaupés, Serra Wabeesee, left bank below Bela Vista, between Ipanoré and confluence with Rio Negro. "Epiphyte, Flowers blue." November 17, 1947. *R. E. Schultes & J. Murça Pires 9141* (Hb. Ames 67529).—Estado do Amazonas, Rio Negro, São Felipe and vicinity. Igarapé Imutá. opposite mouth of Rio Issana. "Epiphyte with flowers light bluish." April 4–7, 1948. *R. E. Schultes & F. López 9765* (Hb. Ames 68527).

COLOMBIA: Comisaría del Vaupés, Río Vaupés, mouth of Karurú, along banks of creek. Altitude about 230 m. "Epífita; flor grande, azul pálido; ginostemo morado y blanquecino." September 27, 1939. *J. Cuatrecasas 7055* (U. S. Nat. Herb. 1796667).—Comisaría del Amazonas, Río Karaparaná, between the mouth and El Encanto. Altitude about 150 m. "Epiphyte. All of flower lilac except lip brown-lilac." May 22–28, 1942. *R. E. Schultes 3813* (Hb. Ames 67515, 67516).—Comisaría del Vaupés, Río Kananarí, Cerro Isibukurí. Near base of mountain. Altitude about 250 m. "Epiphyte. Flowers blue; lip purplish." June 13, 1951. *R. E. Schultes & I. Cabrera 12510* (Hb. Ames 68219). Same locality and date. *Schultes & Cabrera 12511* (Hb. Ames 68220).—Comisarías del Vaupés and Amazonas, Río Apaporis, entre el río Pacoa y el río Kananarí, Soratama. Altitude 250 m. "Delicate violet. Lip brownish violet. Epiphyte." June 21, 1951. *R. E. Schultes & I. Cabrera 12739* (Hb. Ames 68408). Same locality. June 25, 1951. *Schultes & Cabrera 12815* (Hb. Ames 68407). Same locality. June 26, 1951. *Schultes & Cabrera 12837* (Hb. Ames 68409). Same locality. July 4, 1951. *Schultes & Cabrera 12882A* (Hb. Ames 68221). Same locality. July 5, 1951. *Schultes & Cabrera 12892* (Hb. Ames 68413).—Comisaría del Vaupés, Río Pira-paraná, Cano Oo-mooña. "Epiphyte, Fl. blue." September 3, 1952. *R. E. Schultes & I. Cabrera 17149* (Hb. Ames 68547, 68548).—Comisaría del Vaupés, Río Piraparaná, Caño Teemeeña. "Epiphyte. Flowers blue." September 6, 1952. *R. E. Schultes & I. Cabrera 17255* (Hb. Ames 68420).—Comisaría del Vaupés, Río Paca, Wacaricuara and vicinity. Altitude about 650 feet. "Epiphyte. Flowers pale bluish." June 1–3, 1953. *R. E. Schultes & I. Cabrera 19517* (Hb. Ames 68406). Comisaría del Vaupés, Río Kuduyarí, along banks. "Epiphytic, crawling. Flowers blue with purple-brown lip. Floral axis brown-purple. In shade." June 23–26, 1958, *H. García-Barriga, R. E. Schultes & H. Blohm 15783* (Hb. Ames 69350). Same locality and date, *H. García-Barriga, R. E. Schultes & H. Blohm 15784* (Hb. Ames 69349). Same locality and date, *H. García-Barriga, R. E. Schultes & H. Blohm 15785* (Hb. Ames 69348). Same locality and date, *H. García-Barriga, R. E. Schultes & H. Blohm 15787* (Hb. Ames 69347). Same

locality and date, *H. García-Barriga, R. E. Schultes & H. Blohm 15790* (Hb. Ames 69346). Same locality and date. *H. García-Barriga, R. E. Schultes & H. Blohm 15793* (Hb. Ames 69345). Same locality and date. *H. García-Barriga, R. E. Schultes & H. Blohm 15796* (Hb. Ames 69344). Same locality and date. *H. García-Barriga, R. E. Schultes & H. Blohm 15816* (Hb. Ames 69343).—Comisaría del Vaupés, Río Kuduyari, near Savannah Yapobodá, June 26, 1958, *H. García-Barriga, R. E. Schultes & H. Blohm 16021* (Hb. Ames 69342).—Comisaría del Vaupés, Río Kubiyú, June 30, 1958, *H. García-Barriga, R. E. Schultes & H. Blohm 16062* (Hb. Ames 69341).

VENEZUELA: Territorio del Amazonas, Río Orinoco, Esmeraldas. "In arboribus." No date. *Bonpland 1189.* (Hb. Reichenb. 40587).—Territorio del Amazonas, Río Cuao, [affluent of] Río Orinoco. Altitude 125 m. "Terrestrial. 5 outer perianth members pale blue; lip deep purple mauve; column wings reddish." November 25, 1948, *B. Maguire & L. Politi 27393.* (Hb. N. Y. B. G.; Hb. Ames 68210).—Territorio del Amazonas, Ríos Pacimoni-Yatua [affluents of] Casiquiare, flooded forest along uppermost Río Yatua. Altitude 100–140 m. "Epiphyte on living tree trunk, forming vine 1 m. long. Inflorescence purplish; perianth blue, the lip copper-purplish; column purple basally, white apically." December 12, 1953. *B. Maguire, J. J. Wurdack & G. S. Bunting 36762* (Hb N. Y. B. G., Hb. Ames 67820A, 68210B).—Territorio del Amazonas, Ríos Pacimoni-Yatua [affluents of] Casiquiare. Along uppermost Río Yatua, above mouth of Río Yacibo. Altitude 100–140 m. "Epiphyte. Flowers blue-lavender; lip wine-colored." January 30–31, 1954, *B. Maguire, J. J. Wurdack & G. S. Bunting 37448* (Hb. N. Y. B. G., Hb. Ames. 67820, 68210A).

Aganisia cyanea ranges throughout the northwestern Amazon of Brazil and Colombia and the headwaters of the Orinoco in Venezuela. Its centre of distribution appears to lie along the Rio Vaupés and its tributaries, where it is very abundant, but collections also indicate that it is not uncommon in the Territorio del Amazonas in Venezuela.

In the forest, *Aganisia cyanea*, with its pale bluish and moderately large flowers, is indeed a thing of rare beauty where colours—especially blues—are seldom in evidence. The orchid climbs up trunks and branches in the densest part of the riparine forests which, during part of the year, is deeply flooded. The repent rhizome may reach a length of fifteen or even twenty feet. It might be interesting to reproduce here Spruce's field notes concerning the type collection of *Aganisia cyanea*, since they seem never to have been published. Exclusive of a detailed description of the flower, Spruce wrote: "R. da cachᵃ on tree trunks by a forest stream. Stems jointed, applied to bark of tree, here and there producing a small bulb and a stalked leaf, and clad with persistent fibres of (bulb-) sheath. Lvs. thinnish, ribbed, elongate-obov. abruptly apic. ac. Axillary few-fld., racemes 12 in. with membr. bracts. Fls large, explan. Seps & pets. subeq., suborbic., apci., light blue (paler within). Lip light brnsh. [= brownish]—purp. with pale veins. Column with 2 cuneate wings at apex; back & wings streaked with red."

In its floral structure, *Aganisia cyanea*, whose flower is very much larger than that of any other species, would seem to stand in an intermediate position between *A. pulchella* and *A. fimbriata*. This is especially true of the structure of the lip.

In 1886, Reichenbach filius referred to "*Aganisia coerulea* Rchb. f.," which "as the *Acacallis coerulea* of Dr. Lindley, is, no doubt, the best Orchid gathered by Dr. Spruce. It was found on the Rio Negro in 1851 by this excellent traveller, and is his No. 1790." Thus, through the citation of Spruce's number as well as from Reichenbach's description, we know that he erroneously applied this name to *Aganisia cyanea*,

a most unfortunate happening, since his name *Aganisia coerulea*, published ten years before, referred to a wholly different species, now considered to be synonymous with *A. fimbriata*.

2. AGANISIA FIMBRIATA Reichenbach fil. in Gard. Chron., n.s., 2 (1874) 452; Cogniaux in Martius Fl. Bras. 3, pt. 5 (1902) 523.

Aganisia coerulea Reichenbach fil. in Gard. Chron. n.s., 6 (1876) 2, 226; Williams, Orch. Grow. Man., ed. 7 (1894) 94, t.; Kew Bull. 4 (1896) 13; Cogniaux in Martius Fl. Bras. 3, pt. 5 (1902) 522.

Aganisia Oliveriana Reichenbach fil. in Gard. Chron. n.s., 9 (1878) 1, 558; Xenia Orch. 3 (1883) 52, t. 223; Kew Bull. Suppl. 4 (1896) 13; Cogniaux in Martius Fl. Bras. 3, pt. 5 (1902) 521.

Acacallis Oliveriana (Rchb. f.) Schlechter. Die Orch. (1914) 419; in Orchis 12 (1918)' 15; Hoehne, Fl. Brasilica 12, pt. 7 (1953) 164, t. 70.

Acacallis fimbriata (Rchb. f.) Schlechter in Orchis 12 (1918) 10; Hoehne, Fl. Brasilica 12, pt. 7 (1953) 165.

Acacallis coerulea (Rchb. f.) Schlechter in Orchis 12 (1918) 14; Hoehne, Fl. Brasilica 12, pt. 7 (1953) 163, t. 69.

Epiphytic herb. Rhizome scandent or long-repent, covered with distichous, appressed sheaths (especially in young state), 6–9 mm. in diameter. Pseudobulbs about 5 cm. apart, fusiform or long-cylindric, slightly beaked, covered (initially at least) by long, membranaceous, accrescent sheathing bracts, 5–7 cm. long, usually 1-foliate. Leaf firmly membranaceous, elliptic to oblong-lanceolate, acute or acuminate, basally cuneate, 18–30 cm. long, 6–7.5 cm. wide, with 5–7 prominent veins beneath; petiole rather stout, channelled, up to 8 cm. long. Inflorescence long-pedunculate, usually about one-half as long as leaf or sometimes shorter, nodding, laxly 2- to 9-flowered. Bracts lanceolate, about 10 mm. long. Flowers large, conspicuous, sometimes pale yellow and white with pale blue-violet lip, often with reddish or dark blue markings. Sepals and petals spreading. Sepals elliptic to obovate, subacute, slightly undulate, 15–22 mm. long, 9–14 mm. wide; lateral sepals somewhat oblique. Petals obovate to orbicular-ovate, acute or almost rounded, basally cuneate, up to 18 mm. long, 13 mm. wide. Lip short-clawed, 3-lobed, 9–14 mm. long (including claw); lateral lobes erect-spreading, minute, triangular-dentiform, usually subacute, 0.7–15 mm. long; mid-lobe membranaceous, deeply concave to subsaccate, flabellate (sometimes suborbicular), basal margins entire, lateral margin deeply fimbriate, often lightly emarginate apically, 8–11 mm. long, up to 11–20 mm. wide; callus fleshy, triangular-lobulate, 2.5–3 mm. high. Column erect, stout, 5–7 mm. long, semiterete, above with 2 membranaceous, triangular or subquadrate auricular wings.

BRAZIL: No precise locality. Cult. and flowered at Hamburg Bot. Gard. No date. (TYPE of *Aganisia Oliveriana* in Hb. Reichenb. 33794, 40589).—Estado do Pará, Districto Acará, Thomé Assú, Agua Branca, "On trunk of sapling in forest. Perennial herb. Flower lilac." *Y. Mexía 5956a* (Hb. Univ. Cal.).—Estado do Amazonas, Igarapé da Cachoeira Alta Umido. Mata virgem. August 7, 1956. *Ernani 4051* (Hb. Garay 6162).

BRITISH GUIANA: Demerara (cultivated in England) *J. F. Salter s.n.* (TYPE in Hb. Reichen. 40596).

COLOMBIA: Comisaría del Amazonas, Río Karaparaná, Entre Ríos. "A monophyllous orchid; flattened ovoid pseudobulbs; flowers white shot with blue." October 1910, *W. Fox 35* (Hb. Kew).

PERU: Departmento de Loreto, Mishuyacu, near Iquitos. Altitude 100 m. In forest. "Fls. pale violet." *Klug 530* (U. S. Nat. Herb. 1455529).—Departa-

mento de Loreto, near Iquitos. Altitude 100 m. "In virgin forest." June, 1925. *G. Tessmann 5156* (Hb. Berol., photograph and analytical drawing in Hb. Ames 37620).—Departamento de Loreto, Mishuyacu, near Iquitos. Altitude 100 m. "Epiphyte. 3 sepals pale blue; 2 sepals pale blue with deeper stripes. Column white. Lip pale blue with deep blue fringes." September 24–28, 1929, *E. P. Killip & A. C. Smith 29984* (Hb. Ames 62079).—Departamento de Loreto, Mishuyacu, near Iquitos. Altitude 100 m. Forest. "Flowers white and rose-violet." April 1930, *G. Klug 1239* (Hb. Field Mus. 625002; U. S. Nat. Herb. 1456250).—Departamento de Loreto, Mishuyacu, near Iquitos. Altitude 100 m. Forest. "Fls. blue-lilac." April 1930. *G. Klug 1257* (U. S. Nat. Herb. 1456262; Hb. Field Mus. 624990).—Departamento de San Martin, Chazuta, Rio Huallaga. Altitude about 260 m. "Flowers pale and dark lilac." March 1935, *G. Klug 3985* (Hb. Kew; U. S. Nat. Herb. 1458411; Hb. Gray 6001).

Specimen number *40589* from the Reichenbach Herbarium, the type of *Aganisia Oliveriana*, was prepared from cultivated material with no indication as to the country of origin of the plant. In his description of *Aganisia Oliveriana*, however, Reichenbach stated that the species came from Brazil. The type and only collection of *Aganisia fimbriata* consists of two flowers and several excellent floral drawings. There is, attached to the type specimen, a latter from J. T. Salter, Esq., of Laurie Park, Sydenham, England, to Reichenbach, which gives data of interest from a taxonomic point of view: "In answer to your enquiry concerning the habits of *Aganisia* named by you *fimbriata*, I decidedly name it a stiff climber. The stem ½ inch to ⅜ thick with bulbs (pseudo) rather close to stem at 2 inches apart alternate sides, shape of pseudobulbs of an elongate oval terminated with 3 to 4 leaves, length of pseudobulbs 1½ inches, width about ½ inch, leaves leathery, something after a weakly growth of *Coelogyne Lowii*, when received was clasping a small branch firmly (in close contact) by its rooty stem—a native of Demerara, was sent over with *Paphinia cristata* . . . the specimen sent was from a very weakly break, the bulb hardly one-sixth the size of the imported ones makes me think we can hardly judge the value of the plant as a spike with 18 to 20 flowers would be very pretty."

A study of the flowers of the type of *Aganisia fimbriata* in the Reichenbach Herbarium indicates that the differences between this concept and those later described by Reichenbach as *A. coerulea* and *A. Oliveriana* are of such a trivial nature that not even varietal distinctions could reasonably be established for them. Therefore, I am reducing *Aganisia coerulea* and *A. Oliveriana* to synonymy under the earlier *A. fimbriata*. Sketches made by Reichenbach and preserved in his herbarium show the lip of *Aganisia fimbriata* as very deeply saccate or even hemispherical, but careful examination of one of the two flowers of the type boiled soft and floated out in water, convinces me that the lip has been incorrectly interpreted and that it is hardly subsaccate. The flower is smaller, and the lip tends to be somewhat more deeply concave than in our ample material which has hitherto been referred to *Aganisia coerulea*. A glance at the accompanying plate, nevertheless, will show that there are, in reality, no significant differences between the two concepts.

3. AGANISIA PULCHELLA Lindley in Bot. Reg. 25 (1839) Misc. 65 p. 45; *ibid*. 26 (1840) t. 32; Beer, Prakt. Stud. Orch. (1854) 187; Reichen-

bach fil. in Walpers Ann. Bot. 6 (1862) 505; Du Buysson, L'Orchid. (1878) 180; Stein, Orchideenb. (1892) 66; Veitch, Man. Orch. Pl. 9 (1893) 69; Bois, Orchid. (1893) 128; Williams, Orch.-Grow. Man., ed. 7 (1894) 94; Linden, Orch. Exot. (1894) 577; Cogniaux in Martius Fl. Bras. 3, pt. 5 (1902) 521; Broadway in Orch. Rev. 34 (1926) 134; Schlechter in Orchis 12 (1918) 10, fig. 1; Hoehne, Icon. Orch. Bras. (1949) 221, t. 211; Hoehne, Fl. Brasilica 12, pt. 7 (1935) 158, t. 68; A. D. Hawkes in Orch. Journ. 2 (1953) 180.

Aganisia brachypoda Schlechter in Beih. Bot. Centralbl. 42, Abt. 2 (1925) 126; Hoehne, Fl. Brasilica 12, pt. 7 (1953) 159.

Epiphytic herb, often with very long, creeping rhizome up to 3–4 mm. in diameter. Pseudobulbs small, about 2 cm. long, covered (initially at least) by long, papery, accrescent sheathing bracts. Leaf firmly membranaceous, elliptic or oblong-elliptic, acuminate, 10–18 cm. long, 3–4 cm. wide· petiole slender, 4–6 cm. long. Inflorescence short-pedunculate, erect, 3- to 8-flowered, shorter than the leaves. Bracts triangular-ovate, 3–4.5 mm. long. Flowers showy, 3 cm. in diameter, white with lip tinged with yellow (crest) and basally red- or purple-spotted. Sepals and petals spreading, subequal, oblong or oblong-ovate, acutish, 12–13 (rarely up to 19–20) mm. long, 7–8 mm. wide. Lip subsessile, 3-lobed; basal portion ("hypochile") deeply concave, somewhat rhombiform with erect sides; mid-lobe ("epichile") suborbicular, ovate or subtriangular, entire or very minutely crenulate, apically rounded or obtuse, 11–12 (rarely up to 15) mm. long, 10–12 mm. wide; lateral lobes broadly rounded, obtuse or subacute, 2–2.5 mm. long; callus apparently yellow, fleshy, cristate, irregularly verrucose, 1.5 mm. high. Column erect, semiterete, 5 mm. long, footless, apically with auriculate, falcate wings.

BRITISH GUIANA: *E. F. im Thurn C.N. 13* (Hb. Kew).—East Coast Water Conservancy, southeast of Georgetown; canal southeast of Lamaha Stop-off. "On trees in wet forest." November 27, 1919. *A. S. Hitchcock 16992* (Hb. Ames 17658; Hb. Gray 5999; U. S. Nat. Herb. 1056182; Hb. N. Y.).—Vicinity of Bartica, on the Essequibo River, lat. 6°25'N. "Flowers white with yellow and purple spots." September 3–12, 1922. *J. S. de la Cruz 2000* (Hb. Ames 68586; Hb. Gray 6000; U. S. Nat. Herb. 1190427; Hb. Field Mus. 542878; Hb. N. Y.).—Northwest District, Anabisi River. "Epiphyte. Flowers white and yellow." February 15, 1922. *J. S. de la Cruz 1370* (Hb. Ames 22983; Hb. N. Y.).—Upper Mazarumi River, Kamakusa. November 4, 1922, *Herbert Leng 21* (Hb. N. Y.).—Pakaraima Mountains, Membaru-Kurupung Trail. Altitude 1000 m. "Terrestrial or low epiphyte. Flowers white. Lip with yellow spot in centre and reddish processes at base. Locally frequent in *Cunuria* forest. October 29-November 1, 1951. *B. Maguire & D. B. Fanshawe 32341* (Hb. Ames 68526).

DUTCH GUIANA: Road from Moengo-tapoe to Grote Zwiebelzwamp. October 8. 1948. *J. Lanjouw & J. Lindeman 730* (Hb. Utrecht 073510).—Nassau Mountains, forested slope and summit, 400–500 m. alt., Morowijne River. "Epiphyte. Perianth green-white, lip white, bronze only at small lateral basal lobes." March 11, 1955. *Bassett Maguire 40792* (Hb. N. Y. Bot. Gard.).

TRINIDAD: Surinam River, Jodensavanne-Mapane Kreek area. "Flower white, labellum white with large yellow spot and purple spots and brown-red hairs at the base." May 5, 1953, *J. C. Lindeman 3956* (Hb. Ames 68439).—Aripo Savannah. "On tree in forest." March 5, 1920. *Dorothy Coker & W. R. Rowland s.n.* (Hb. Ames 68214; Hb. N. Y. Bot. Gard.).

VENEZUELA: Estado de Bolívar, 102 km. de El Dorado hacia Santa Elena. "Trepadora abundante en selva higrofítica macrotérmica." December 29, 1956. *E. Foldats 2675* (Hb. Ames 68529; Hb. Nac. Venez.).

AGANISIA
pulchella
Lindley

cyanea
(*Lindley*)
Reichb. fil.

fimbriata
Reichenbach fil.

E.W.Smith

There are in the Reichenbach Herbarium (40586) four collections of different provenience, one of which was from cultivated material. The labels are so incomplete or confused that they cannot be cited separately under countries.

Aganisia pulchella, the type species of the genus, is native to Trinidad and British and Dutch Guiana. In Trinidad, it is known only from the sandy savannah regions in the central part of the island. Dr. Wilbur G. Downs and Schultes collected a sterile specimen in July, 1958, in the Aripo Savannah; this is being cultivated but has not as yet flowered. Surprisingly few collections have been made in the field in the more than a century since this species was first described. It may also be registered through *Huebner 168* from the northwest Amazon of Brazil. Foldats has identified a second Venezuelan collection, *Cardona 2337* (Cerro Acopán, Estado de Bolivar) as representing *Aganisia pulchella*.

Perhaps the most distinct of the species of *Aganisia*, *A. pulchella* was thought for many years to be the only member of the genus. It is apparently the smallest representative of *Aganisia*, both vegetatively and florally. Several major floral characters, set forth in the key, further separate *Aganisia pulchella* from the other known species.

I have not been able to examine typical material of *Aganisia brachypoda* which was destroyed in the recent war. A study of its description, however, suggests to me that there is little, if any, difference of a fundamental nature upon which to erect a distinct species-concept. Schlechter said that his *Aganisia brachypoda* differed from *A. pulchella* by having shorter racemes with three or four (instead of four to six) flowers; by having smaller flowers which were entirely white (instead of having a cherry-red spot on the inner part of the lip; and in having longer and narrower leaves. *Aganisia pulchella* is usually footless, and Schlechter has indicated, by his choice of specific name, that the type of *A. brachypoda* possessed a short foot. The structure of the lip, according to Schlechter, differed from that of *Aganisia pulchella*, but I have been unable to find in his description of *A. brachypoda* any real differentiating characters in this organ. The type of *Aganisia brachypoda* (*Huebner 168*) was collected at Taracuá, on the Rio Uaupés, at the mouth of the Rio Tikié in Amazonian Brazil. Taracuá, the most westerly locality for *Aganisia pulchella*, lies not far from Ipanoré, Spruce's type locality of *Aganisia cyanea*, where many elements known also from British Guiana have been found. We, therefore, might expect *Aganisia pulchella* to occur in the northwestern Amazonian area of Brazil. It may, likewise, turn up in Colombian territory.

EXCLUDED SPECIES

Aganisia boliviensis Rolfe ex Rusby in Bull. N. Y. Bot. Gard. 4 (1907) 448 = *Koellensteinia eburnea* (Barb.-Rodr.) Schlechter in Orchis 12 (1918) 28.

Except for a rather congested inflorescence, the type specimen *Bang 2909* in N. Y. Bot. Gard.) of *Aganisia boliviensis* (*Koellensteinia boliviensis* (Rolfe ex Rusby) Schlechter loc. cit. 32) would seem easily to be accommodated in the concept *K. eburnea*, which, according to Schweinfurth, may "be referable to *K. ionoptera* (Lind. & Reichenb.

fil.) Nichols, but at present the material at hand is insufficient to form a definite conclusion".

Aganisia brachystalix (Reichenb. f.) Rolfe in Orch. Rev. 22 (1914) 200 = *Otostylis brachystalix* Reichenb. f.) Schlechter in Orchis 12 (1918) 39, t. 5.

Reichenbach's *Aganisia brachystalix* agrees with the genus *Otostylis* as set up by Schlechter.

Aganisia graminea (Lindl.) Bentham & Hooker fil. Gen. Pl. 3 (1883) 544 = *Koellensteinia graminea* (Lindl.) Reichenbach fil. in Bonplandia 4 (1856) 323.

Aganisia graminea is merely a synonym of the widespread *Koellensteinia graminea* of Peru, Venezuela, Amazonian Brazil, the Guianas and Trinidad.

Aganisia ionoptera (Lind. & Reichenbach fil.) Nichols Dict. Gard. 1 (1888) 35 = *Koellensteinia ionoptera* Linden & Reichenbach fil. in Gard. Chron. (1871) 1471.

This concept is definitely referable to *Koellensteinia*.

Aganisia Kelneriana (Reichb. f.) Bentham in Bot. Mag. (1892) sub t. 7270 = *Koellensteinia Kellneriana* Reichenbach fil. in Bonplandia 2 (1854) 17, 281.

There can be no doubt that the concept described as *Aganisia Kelneriana* is referable to *Koellensteinia*. *Koellensteinia Kellneriana* may later prove to be synonymous with *K. eburnea*, but, for the present, I shall refer *Aganisia Kelneriana* to *K. Kellneriana*.

Aganisia lepida Linden & Reichenbach fil. ex Reichenbach fil. Beitr. Orchideenk. 15 (1869) t. 5a = *Otosytlis lepida* (Lind. & Reichenb. fil.) Schlechter in Orchis 12 (1918) 40.

Aganisia lepida represents a concept in Schlechter's genus *Otostylis*, in which it would seem to constitute a distinct species.

Aganisia venusta (Ridl. ex Oliver) Rolfe ex Hooker fil. in Bot. Mag. (1892) sub t. 7270 = *Otostylis alba* (Ridl. ex Oliver) Summerhayes in Kew Bull. 1951 (1951) 293.

A complete synonymy of *Otostylis alba*, to which *Aganisia venusta* (*Zygopetalum venustum*) Ridley (in Trans. Linn. Soc., ser. 2, Bot. 2 (1887) 283, t. 47, fig. 1–6)) is referred, may be found in Summerhayes (loc. cit. 293).

The Genus Poria in North America

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Species of fungi that occur upon wood are predominantly Hymeno-mycetes, among which the Polyporaceae is a very large and economically important family. Polypores that persistently grow closely attached to their substratum, *i.e.*, are resupinate, may be placed in the genus Poria. The genus is second only to the genus Polyporus in its diversity and abundance, and it is the most difficult one taxonomically. Many biological and pathological investigations have been neglected because of difficulties in identifying the organisms. Species in genera other than Poria, notably in Polyporus and Trametes, may initially develop resupinate sporophores and then could be confused with true porias. Interpolation of the resupinates among similar species in genera based on a natural classification would be the ideal system; as yet, however, not enough detailed knowledge of these groups has been assembled. The identification of the genus on an easily observed characteristic has the practical merit of ready application.

Previous to 1918 work in the genus Poria in America was largely an accumulation of proposals of new species, and attempts to relate the American flora to the European one. Exact morphological studies were needed. These were initiated in Europe by Bresadola and Romell, followed in America by Overholts (1918, 1923) and Lowe (1947, 1948, 1949, 1956). Compilations of the reported flora were prepared by Murrill (1919, 1920a-b, 1921a-b) and by Baxter (1932, 1933). Technical treatments of the Poria flora of limited areas have been published for the central Rocky Mountains and the Pacific Northwest (Gilbertson, 1956), for Oregon (Cooke, 1942), for New York (Lowe, 1946), and for Pennsylvania (Overholts, 1942). Baxter's series of papers (1927–55) is the only published work which treats the occurrence of selected species of Poria throughout North America.

In Poria the lack of a pileus eliminates many macroscopic characteristics helpful in the taxonomy of pileate species. Useful external characteristics are the presence or absence of rhizomorphs, the color of the pore surface and the size of the pores. Taste is a very helpful field character. Many species are restricted to a substratum of the wood of either gymnosperms or angiosperms. Unless otherwise specifically stated all specimens were found on a woody substratum and this is to be understood where the substratum is stated. Consistency is a useful characteristic which must, in large measure, be learned by reference to named specimens. In Poria the segregation of the species with brown tissue from those with white or brightly colored tissue is of fundamental taxonomic importance, and would justify generic separation. The white and brightly colored species should be considered in one group, however, as the interrelations are certainly very close, and some species vary over this range of color.

All microscopic examinations were made from sections first mounted

in alcohol to remove air, then placed in 2 percent potassium hydroxide solution. The nature of the context hyphae within the white and brightly colored group seems to be the most useful character for the primary segregation of the species, but the variations in hyphae introduce some difficulties. Species with septate hyphae usually have only one hyphal type present; those with the principal hyphae nonseptate (or clamped) usually have one or more other types in varying abundance. Future studies may lead to a more precise employment of hyphal characteristics, but such information has not yet been assembled. Cystidia vary much in abundance, and the intergrading of cystidioles with cystidia may be confusing. All spore measurements are of basidiospores. In general satisfactory determinations are the product of careful microscopic study and of comparison with accurately determined specimens.

This is a preliminary treatment, designed to make available information that has been accumulating for more than 15 years, and to provide a means of identification of the species known from North America. One hundred thirty-one species of Poria are recognized as valid to the flora of North America. No new species are described; one new combination is proposed (No. 10, *Porogramme albocincta*). The following are proposed for synonymy for the first time, as far as known:

Leptoporus asiaticus Pilát=80. *P. sericeomollis*
Polyporus griseoalbus Peck=69. *P. rhodella*
viridans Berk. & Br.=69. *P. rhodella*
Poria coniferarum Baxt.=91. *P. bombycina*
eyrei Bres.=102. *P. versipora*
flavida Murr.=83. *P. radiculosa*
floridae Murr.=19. *P. lacteimicans*

Poria grandis Overh.=82. *P. albolutescens*
greschikii Bres.=37. *P. xantha*
latitans Bourd. & Galz.=102. *P. versipora*
notata Overh.=113. *P. subvermispora*
ossea Baxt.=88. *P. rhoadsii*
parksii Murr.=60. *P. terrestris*
washingtonensis Murr.=54. *P. similis*

Types or authentic specimens have been examined for all species except those enclosed in brackets. Grateful thanks are due the directors or curators who permitted access to or loan of many specimens under their care at the following institutions: The Farlow Cryptogamic Herbarium at Cambridge, Mass.; Muséum National d'Histoire Naturelle, Laboratoire de Cryptogamie, Paris, France; The National Fungus Collections at Beltsville, Maryland; the New York Botanical Garden, New York, N. Y.; Riksmuseet, Stockholm, Sweden; and Royal Botanic Garden, Kew, England. Thanks are also due to many other curators who loaned certain specimens under their care. Both the microscopic studies and distribution records are based in part on work done while financed by grants from the National Science Foundation, and from the Mycological Society of America. Especially grateful acknowledgement is made to the late Dr. L. O. Overholts, who, in the early phases of my study, freely shared his personal knowledge of the group, and his manuscripts on Poria.

SYNOPSIS OF THE SPECIES

Section 1. SPOROPHORES WHITE OR BRIGHTLY COLORED, AT LEAST WHEN FRESH, NOT BROWN AND THE TISSUE NOT DARKENING IN KOH SOLUTION (for brown species see No. 116)

1a. Pores arising as papillae, with age these opening and sporophore becoming poroid

1. *Porotheleum fimbriatum* (Pers. ex Fries) Fries. Sporophore membranous, rhizomorphic. On gymnosperms and angiosperms, widely distributed. The genus has been fully treated by Cooke in Mycologia 49: 680–693. 1957.

1b. Pores open and hymenium exposed from the first

2a. Principal subiculum hyphae without septa (with septa, see No. 49; with clamps see No. 77)

3a. Spores oblong-ellipsoid to globose, not cylindrical (for 3b, see No. 26)

4a. Basidia usually 5–8 μ or more in diam.

5a. Sporophore when dry soft-coriaceous; spores echinulate

2. *Poria lenta* Overh. & Lowe. Spores 5–6 x 4–5 μ. On gymnosperms in Ont., N. Y., Tenn., Colo., Idaho, and Wash.

3. *Poria avellanea* Bres. Spores 3–5 x 2.5–4μ. On wood of angiosperms in S. Car., Fla., and Jamaica. Syn.: *heteromorpha* Murr.

5b. Sporophore when dry corky to rigid; spores smooth

6a. Tramal hyphae distinctly larger than most of context hyphae

4. *Poria calkinsii* Murr. On wood of angiosperms in Fla.

6b. Tramal hyphae similar to or more narrow than the context hyphae

7a. Spores rounded at both ends (compare also 95. *P. overholtsii*)

5. *Poria conferta* Overh. Tubes not markedly discolored when dry. On gymnosperms and angiosperms in N. Y. and Pa.

6. *Poria discolor* Overh. Tubes strongly discolored when dry. On angiosperms in Vt., N. Y., Pa., Tenn., and Mich.

7b. Spores frequently truncate at one end

7. *Poria subacida* (Peck) Sacc. Spores 4–5.5 μ long; pores 2–4 per mm.; context hyphae highly variable, 1.5–5 μ in diam. Widely distributed on gymnosperms and angiosperms. Syn.: *colorea* Overh. & Englerth, *fuscomarginata* Berk., *omaema* Berk., *ornata* (Peck). This species intergrades with the next.

8. *Poria tenuis* (Schw.) Cooke. Spores 5–7 μ long; pores 3–6 per mm. On angiosperms, widely distributed. Syn.: *beaumontii* Berk. & Curt. The yellow forms of this have been named *P. pulchella* (Schw.), *P. holoxantha* Berk. & Cooke, and *P. vitellina* (Karst.).

9. *Poria unita* (Pers.) Cooke. Spores 4–7 μ long; pores 5–8 per mm. On angiosperms, widely distributed. Syn.: *alboincarnata* (Pat. & Gaill.), *cremor* (Berk. & Curt.), *dryina* (Berk. & Cooke), *limitata* (Berk. & Curt.), *medullapanis* (Pers.), *tomentocincta* Berk. & Rav., *xylostromatis* (Fuckel). *P. fulviseda* Bres. is a probable synonym; it grows on wet substrata and has rather small spores, 4–5 x 2.5–3.5 μ.

4b. Basidia rarely over 5 μ in diam.

8a. Hymenium restricted to base of tubes (genus Porogramme)

10. **Porgramme albocincta** (Cooke & Massee) Lowe, comb. nov. Pore surface blue. In La., Mexico, and P. R., widely distributed in the tropics on angiosperms. Syn.: *aurantiotingens* (Ellis & Macbride), *buttneri* Henn., *fuligo* (Berk. & Br.), *glauca* Pat.

8b. Hymenium lining walls of tubes (genus Poria)

9a. Cystidia present

10a. Pore surface more or less pinkish

11. *Poria radula* (Pers. ex Fries) Bres. Rhizomorphic; pores 2–4 per mm. On angiosperms in N. Y., Colo., Idaho, and Wash. Syn.: *eupora* var. *subfimbriata* (Rom.).

12. *Poria eupora* (Karst.) Cooke. Not rhizomorphic; spores oblong-ellipsoid to ellipsoid; connective hyphae clamped. On angiosperms, widely distributed. Syn.: *attenuata* (Peck).

13. *Poria carneopallens* (Berk.) Cooke. Not rhizomorphic; spores ovoid to subglobose, often with flattened sides and appearing more or less tri-

angular; connective hyphae septate. Subtropical and tropical, on angiosperms. Syn.: *fulvobadia* Pat.; ?*porphyrophaea* Bres.—type sterile.

10b. Pore surface white to brownish

14. *Poria fimbriatella* (Peck) Sacc. Rhizomorphic, white to cream. On angiosperms in the eastern U. S. and on the Pacific Coast.

15. *Poria cavernulosa* (Berk.) Cooke. Not rhizomorphic, grayish-vinaceous drying wood brown. On angiosperms in Fla. and Cuba. Resembles resupinate *Polyporus versatilis* (Berk.) Rom. but has small spores, 5 x 2–2.5 µ.

9b. Cystidia absent

11a. Pores 1–4 per mm.; hyphal pegs present

16. *Poria aestivale* Overh. Pores 1- 1.5 per mm. On angiosperms in Ont., N. Y., and Pa.

17. *Poria illudens* Overh. & Lowe. Pores 3–4 per mm.; basidia broadly clavate, 8–11 µ long. On angiosperms and gymnosperms in Ont., Vt., N. Y., and Pa.

18. *Poria niphodes* (Berk. & Br.) Cooke. Pores 3–4 per mm.; basidia narrowly clavate, 11–16 µ long. On angiosperms in the tropics. Syn.: *hondurensis* Murr.

11b. Pores 4–10 per mm.; hyphal pegs lacking (except in No. 19)

12a. Spores minute, 2–3 µ long

19. *Poria lacteimicans* Murr. On angiosperms in Fla. Syn.: *floridae* Murr.

12b. Spores usually 3–5 µ long, or unknown

13a. Context hyphae 2.5–5 µ or more in diam.; northern

20. *Poria humilis* Murr. White, discoloring somewhat on drying; rhizomorphic; bitter; spores 5–6 x 3–3.5 µ. On rotten wood and over mosses in N. E., further distribution uncertain. An inadequately known species. Isotype material at the Farlow Herbarium is a better sample than the type at Kew. Syn.: *incrustans* (Berk. & Curt.), [?*herbicola* Baxt.].

21. *Poria fissiliformis* Pilát. Cream, drying yellowish; context hyphae 3–5 µ in diam.; spores short-oblong to ellipsoid, 1.5–2.5 µ wide. On angiosperms in the eastern U. S. *P. confusa* Bres. is very similar but has spores 3–3.5 µ wide.

22. *Polyporus semisupinus* Berk. & Curt. Similar to the next above but with shorter tubes and spores oblong-ellipsoid to ovoid, 2–3 µ wide. Common in the resupinate condition (*Poria pallescens* ("Karst.")) on angiosperms in the eastern U. S. Apparently the same as *P. byssina* (Pers.) Rom. of Eriksson determinations.

13b. Context hyphae 1.5–3 µ in diam.; southern

23. *Poria flavipora* (Berk. & Curt.) Cooke. Pore surface yellow or orange, fading on drying; tissue unchanged in KOH solution. On angiosperms in Fla.

24. *Poria phlebiaeformis* Berk. Pore surface orange, usually fading on drying; tissue violaceous in KOH solution. In Fla. and Cuba. Compare 88. *P. rhoadsii*.

25. *Poria borbonica* Pat. Pore surface pale glaucous blue. On angiosperms in Fla., La., P. R., and Jamiaca. Syn.: *cinereicolor* Murr.

3b. Spores cylindrical, straight or curved, or lunate (or uncertain in Nos. 27, 47, 48)

14a. Cystidia large and conspicuous

26. *Poria rixosa* Karst. Sporophore pinkish; pores 4–6 per mm.; northern. On gymnosperms, widely distributed. Syn.: *dodgei* Murr.

27. *Poria vincta* (Berk.) Cooke. Pinkish; pores 8–9 per mm.; tropical. Spores unknown. On angiosperms in tropical America. Inadequately known. Compare 13. *P. carneopallens*.

28. *Poria luteoalba* (Karst.) Sacc. Cream or yellowish; pores 3–4 per mm. On gymnosperms in eastern North America. Syn.: *flavicans* Karst.; *sinuascens* Pilát.

29. *Poria zonata* Bres. White to cream; pores 1–2 per mm.; context with a variable amount of clamped connective hyphae. On gymnosperms in the northwestern U. S.

14b. Cystidia absent; cystidioles may be present
15a. Basidium cruciately divided (genus Aporpium)

30. *Aporpium caryae* (Schw.) Teix. & Rogers. On angiosperms, widely distributed. Syn.: *argillacea* (Cooke), *canescens* Karst., *pilati* Bourdot, *gilvescens* of American authors, not Bres.

15b. Basidia nonseptate (genus Poria)
16a. Spores more than 2 μ wide
17a. Spores 8–16 μ long, echinulate

31. *Poria papyracea* (Schw.) Cooke. Spores 13–16 x 5.5–7 μ; pores 2–2.5 per mm.; thin-walled hyphae with clamps. On angiosperms and gymnosperms in the eastern U. S. Syn.: *barbaeformis* (Berk. & Curt.).

32. *Poria alabamae* (Berk. & Cooke) Cooke. Spores 8–14 x 3.5–6 μ; pores 4 per mm.; septa lacking. On angiosperms in Fla. and Miss.

17b. Spores up to 10 μ long, smooth

33. *Poria crustulina* Bres. Taste mild; pores 3–4 per mm.; context hyphae 3–5 μ in diam. On gymnosperms, widely distributed. Syn.: *chromatica* Overh.

34. *Poria magnahypha* Overh. Mild; pores 1 or less per mm.; some context hyphae up to 20 μ in diam.; spores 8–10 x 3.5–4 μ. On angiosperms in Pa. and Tenn.

35. *Poria oleracea* Davids. & Lomb. Bitter; somewhat chalky when dry. On Quercus in N. Y. and Md.

16b. Spores 0.5–2 μ wide
18a. Pores 1–3 per mm.

36. *Poria sinuosa* (Fries) Cooke. Context hyphae 2–3 μ in diam.; spores 4–5 x 1–2 μ. On angiosperms, widely distributed.

18b. Pores 4–10 per mm.
19a. Taste bitter

37. *Poria xantha* (Fries) Cooke, sense of Lind. Pore surface usually yellow, often whitening in age or on drying, drying fragile; context hyphae 3–5 μ in diam. On gymnosperms and angiosperms, widely distributed. Syn.: *greschikii* Bres.—a weathered specimen, *sulphurella* (Peck).

38. *Poria oleagina* Overh. White to cream, drying tough; spores 3.5–5 x 1.5–2 μ. On gymnosperms in the eastern U. S.

39. *Poria stenospora* Overh. Grayish-white; spores 8–9 x 1.5–2 μ. On gymnosperms in Washington.

19b. Taste mild or slightly resinous
20a. Spores lunate

40. *Poria lenis* Karst. Pores 5–7 per mm. On gymnosperms, widely distributed. Syn.: *montana* Murr., also probably *earlei* Murr., the type of which is sterile. Spores highly variable, when some or most are allantoid compare 46. *P. sitchensis*.

41. *Poria tenuipora* Murr. Pores 9–10 per mm. On angiosperms in Jamaica.

20b. Spores cylindrical, oblong or allantoid
21a. Sporophore rhizomorphic; spores 2.5–3.5 μ long

42. *Poria alutacea* Lowe. Leathery, separable. On gymnosperms and angiosperms in eastern and western U. S.

21b. Not rhizomorphic; spores 3.5–8 μ long
22a. Pore surface more or less pinkish

43. *Poria subincarnata* (Peck) Murr. Tubes up to 4 mm. long, leathery; hyphal pegs present; without distinctive odor. On gymnosperms, widely distributed.

44. *Poria odora* (Peck) Sacc. Tubes up to 8 mm. long, rigid and brittle when dry; hyphal pegs absent; odor "strong, disagreeable" (Peck). On gymnosperms and angiosperms in the Northeast, its distribution uncertain as it is readily confused with the preceding species and with 45. *P. stellae* and 46. *P. sitchenis*.

22b. Pore surface white to cream, or drying pale brown

45.   *Poria stellae* Pilát.   Context hyphae 4–5 μ in diam.; spores 0.5–1 μ wide. On gymnosperms in the Rocky Mountains.

46.   *Poria sitchensis* Baxt.   Context hyphae 3–5 μ in diam.; spores 1.5 μ wide. Imperfectly known and very similar to the preceding; on wood of angiosperms, apparently rare but widely distributed in the Temperate Zone.

47.   *Poria rimosa* Murr.   Context hyphae 1.5–2 μ in diam.; sporophore rigid and fragile when dry.   On Juniperus in Okla. and N. Mex.   Very similar to and perhaps a form of *P. versipora* with rare clamps on the context hyphae. The allantoid spores reported for the species (Lowe 1947, p. 55) have not been found in a restudy of the type material.

48.   *Poria ferox* Long & Baxter.   Context hyphae 1.5–3 μ in diam.; sporophore tough and corky when dry.   On Juniperus in Ark., Okla., N. Mex., and Ariz.   Very few and not wholly certain spores were seen on the type and all other material of this studied; the fungus may be a form of *Trametes serialis* Fries.

    2b. Principal context hyphae with septa
        23a. Some of context hyphae much inflated, up to 16 μ in diam.

49.   *Poria inflata* Overh.   Spores 4–5 x 2.5–3 μ.   On angiosperms in the eastern U. S.

50.   *Poria cocos* (Schw.) Wolf.   Spores 7–11 x 2.5–3 μ; associated with a sclerotium found in soil.   Widely distributed but rarely found fruiting; very rarely on wood.

        23b. Context hyphae more or less uniform in diameter
            24a. Spores ellipsoid to globose
                25a. Cystidia present
                    26a. Cystidia capitate-incrusted, short

51.   *Poria corticola* (Fries) Cooke.   Context hyphae uniformly 3–4 μ in diam. On angiosperms, widely distributed.   Syn.: *?salviae* (Berk. & Curt.)— type sterile and myriadoporous, *separans* Murr., *?vesiculosa* (Berk. & Curt.)—type sterile and myriadoporous, *vicina* Bres.

52.   *Poria ambigua* Bres.   Context hyphae variable, 3–8 μ in diam.   On angiosperms, widely distributed and ambiguously separated from next above. Syn.:   *cokeri* Murr., *lacerata* Murr., *salicina* Murr., *sumstinei* Seaver.

53.   *Polyporus cuneatus* (Murr.) Zeller.   Frequently resupinate on cedar in the Northwest.   Very soft when dry, and with small spores, 3.5–5 x 3–4 μ.

                    26b. Cystidia clavate-incrusted, long

54.   *Poria similis* Bres.   Cystidia coarsely incrusted; spores 2.5–5 x 2.5–3.5 μ. On angiosperms in central and northwestern U. S. and Canada.   Syn.: *washingtonensis* Murr., *n. nudum*.

55.   *Poria proxima* Bres.   Cystidia finely incrusted; spores 5–6 x 2.5–3 μ.   On angiosperms in Ind.

                25b. Cystidia absent
                    27a. Spores spiny

56.   *Poria trachyspora* Bourd. & Galz.   On angiosperms in Ont., N. Y., Pa., N. Car., Mich., and Iowa.   Sporophore is poroid; otherwise plant is misplaced in Poria.

                    27b. Spores smooth
                      28a. Sporophore soft, drying soft or fragile
                        29a. Spores oblong-ellipsoid to ellipsoid

57.   *Poria fatiscens* (Berk. & Rav.) Cooke.   Tubes drying rigid, fragile; pores 4 per mm.; spores 3–4 μ long.   On angiosperms and gymnosperms, widely distributed.   Syn.:   *fagicola* Bres., *roseitingens* Murr., *semitincta* (Peck), *? subcorticola* Murr.—type sterile, *subviolacea* Ellis & Everh., *tenella* (Berk. & Cooke).

58.   *Poria cubitispora* Murr.   Tubes drying rigid and fragile; pores 7–8 per mm.; spores 2.5–3 μ long.   On gymnosperms in Fla.

59.   *Poria niveicolor* Murr.   Tubes drying very soft, sporophore somewhat membranous; pores 6–7 per mm.; spores 2.5–3 μ long.   On angiosperms in Jamaica.   Compare 19. *P. lacteimicans*.

                    29b. Spores broadly ellipsoid to subglobose
                      30a. Pores 2–4 per mm.

60.   *Poria terrestris* (DC) Sacc. Rhizomorphic, membranous and readily
      separable; tubes usually drying distinctly yellowish. On angiosperms
      and gymnosperms in eastern and western U. S. Syn.: *parksii* Murr.;
      ?millavensis Bourd. & Galz.
61.   *Poria subambigua* Bres. Not rhizomorphic, adnate; tubes whitish to cream
      when dry. On angiosperms, doubtfully of gymnosperms in eastern U. S.
      and Africa. Syn.: *flaccida* Overh., [*?taxodium* Baxt.].

                       30b. Pores 5–6 per mm.

62.   *Poria chrysobapha* (Berk. & Curt.) Cooke. Spores pale yellowish-brown;
      pore surface "golden yellow—inclining to olive" (Berk. & Curt.); tubes
      rigid and rather fragile when dry. Known only in Alabama, from the
      type which is a small inadequate specimen.
63.   *Poria cremeicolor* Murr. Spores hyaline; pore surface cream in color; tubes
      soft-spongy. On angiosperms in Cuba and Jamaica. Syn.: *corioliformis*
      Murr.
64.   *Poria diospyri* Baxt. [Spores hyaline; pore surface white to tan or slightly
      sulphureus. Known only from the type in Okla.]

                28b. Sporophore drying tough, corky or cartilaginous

65.   *Poria sanguinolenta* (Alb. & Schw.) Sacc. Context drying cartilaginous,
      whole sporophore often dark red on drying. On angiosperms, widely
      distributed. Syn.: *decolorans* (Schw.), *nebulosa* (Berk. & Curt.).
66.   *Poria undata* (Pers.) Bres. Context drying cartilaginous; pore surface white,
      drying pinkish; associated with a conspicuous white pocket rot. On
      angiosperms in the eastern U. S. Syn.: *albirosea* Murr., *holoseparans*
      Murr.
67.   *Poria nigrescens* Bres. Context fibrous to corky; pore surface pinkish when
      fresh, darkening where bruised; associated with a uniform white rot.
      On angiosperms and gynosperms, widely distributed.
68.   *Poria albostygia* (Berk. & Curt.) Lloyd. Similar to the preceding but with
      more slender context hyphae 4–5 μ in diam.; probably a resupinate condi-
      tion of a species of Polyporus. Fla. and Cuba.

                24b. Spores cylindrical, short-oblong or allantoid
                  31a. Base of tubes at first formed isolated from each other,
                       joining by radial extension, *i.e.*, cupulate

69.   *Poria rhodella* (Fries) Bres. Spores 3–5 μ long; pore surface extremely
      variable in color, whitish to gray, or greenish, or rosaceous. On angio-
      sperms and gymnosperms. Syn.: *griseoalba* (Peck), *nuoljea* (Rom.),
      ?subbadia Murr.—type sterile, *viridans* (Berk. & Br.).
70.   *Poria purpurea* (Fries) Cooke. Spores 5–9 x 1.5–2.5 μ; pore surface more or
      less reddish when dry. On angiosperms and gymnosperms, widely dis-
      tributed. Very similar to the next except for color. Syn.: *bresadolae*
      Bourd. & Galz.
71.   *Poria reticulata* (Fries) Cooke. Spores 6–10 x 2.5–3.5 μ; pore surface white
      to cream when dry. On angiosperms and gymnosperms, widely
      distributed.

                       31b. Not cupulate
                       32a. Pores 3–4 per mm.

72.   *Poria taxicola* (Pers.) Bres. Cystidioles abundant. On gymnosperms,
      widely distributed. Syn.: *rufa* (Schrad. ex Fries).
73.   *Poria placenta* (Fries) Cooke. Cystidioles lacking. On gymnosperms in
      Michigan. Based on a Bresadola determination; specimen in the Farlow
      Herb. Clamp connections occur on the hyphae in a different interpreta-
      tion of this species.

                       32b. Pores 5–8 per mm.

74.   *Poria spissa* (Schw.) Cooke. Pore surface orange, drying dark red; spores
      allantoid; mild. On angiosperms in eastern North America. Syn.:
      laetifica (Peck), *?oxydata* (Berk. & Curt.)—type sterile.
75.   *Poria alachuana* Murr. Pore surface cream when dry; spores short-oblong;
      context hyphae 3–4.5 μ in diam.; disagreeably resinous. On angiosperms
      in Fla.

76. *Poria ferruginicincta* Murr.   Pore surface sordid yellowish-brown when dry;
     spores short-oblong; context hyphae 4–8 μ in diam.; disagreeably resinous.
     On angiosperms in Fla.

> 2c. Principal context hyphae with clamp connections
>> 33a. Spores becoming more or less brown at maturity

77. *Poria incrassata* (Berk. & Curt.) Burt.   Pore surface becoming more or less
     brown in age and on drying; some of context hyphae distinctly brown.
     On gymnosperms, especially of building timbers, widely distributed.
     Syn.: *pinea* (Peck).

>> 33b. Spores hyaline, echinulate

78. *Poria candidissima* (Schw.) Cooke.   Non-cystidiate; spores oval to globose.
     On angiosperms and gymnosperms, widely distributed. Syn.: *fragillima*
     (Karst.), *hymenocystis* (Berk. & Br.), *onusta* (Karst.), *subtilis* (Schrad. ex
     Fries) of European determinations.

79. *Poria regularis* Murr.   Cystidiate; on angiosperms in N. Car., La., and
     Jamaica.   Syn.: *arachnoidea* Murr., *submollusca* Murr.

>> 33c. Spores hyaline, smooth
>>> 34a. Cystidia present (see also No. 29, *P. zonata*)

80. *Poria sericeomollis* (Rom.) Baxt.   Pore surface white to cream; pores 3–5
     per mm.; spores oblong to oblong-ellipsoid, 1.5–2 μ wide; cystidia small;
     bitter.   On gymnosperms, widely distributed.   Syn.: *asiatica* (Pilát),
     litschaueri (Pilát).

81. *Poria aurea* Peck.   Pore surface "golden-yellow" (Peck), drying yellowish;
     pores 2–4 per mm.; spores oblong-ellipsoid to ellipsoid, 2.5–3.5 μ wide;
     cystidia large.   On gymnosperms in N. Y. and Brit. Col.

>>> 34b. Cystidia lacking
>>>> 35a. Pore surface distinctly colored when fresh or on drying
>>>>> 36a. Sporophore rhizomorphic, yellowish when dry

82. *Poria albolutescens* (Rom.) Egel.   Drying soft; pores 3–4 per mm.; spores
     3.5–4 x 2–2.5 μ.   On gymnosperms, widely distributed.   Syn.: *grandis*
     Overh.

83. *Poria radiculosa* (Peck) Sacc.   Drying rigid; pores 1.5–2.5 per mm.; spores
     5–7.5 x 2.5–3 μ.   On gymnosperms, widely distributed.   Syn.: *flavida*
     Murr. (without rhizomorphs), [*luteofibrata* Baxt.], *subradiculosa* Murr.
     This species is quite variable and the synonymy above should not be
     considered as fully established.   A species in the Northwest, provisionally
     named *P. radiculosa*, agrees in structure but has extremely well-developed
     rhizomorphs.

>>>>> 36b. Sporophore not rhizomorphic; pore surface when dry
>>>>>> pink to red, occasionally yellowish
>>>>>> 37a. Spores 3–5 μ long
>>>>>>> 38a. Pores 2–4 per mm.

84. *Poria rubens* Overh. & Lowe.   Pore surface orange, drying livid red or pur-
     plish.   On gymnosperms, widely distributed.   Syn.: *aurantiaca* var.
     saloisensis Karst.

85. *Poria subrufa* Ellis & Dearn.   Pore surface white, changing to reddish on
     bruising and sordid pale reddish brown when dry.   On angiosperms in
     Ontario.   An inadequately known species.

86. *Poria atrorubens* Baxt.   [White, turning garnet where bruished, drying
     reddish brown; pores 2–3 per mm.   On angiosperms in Ark.   The relation
     of this plant to *P. subrufa* and to other plants which turn red on bruising
     is uncertain.]

>>>>>>> 38b. Pores 4–7 per mm.
>>>>>>>> 39a. Context when dry with a distinct line
>>>>>>>>> at base of tubes

87. *Poria pannocincta* (Rom.) Lowe.   Pale yellow.   On angiosperms, widely
     distributed.   Syn.: [*tacamahacae* Baxt.], [?*viridiuscula* Baxt.], *zameriensis*
     (Pilát).   *P. viridiuscula* is separated from *P. pannocincta* in the original
     description on a color difference in the fresh specimen.

>>>>>>>> 39b. Context homogeneous

88. *Poria rhoadsii* Murr.   Tissue violaceous then decolorate in KOH solution;
     tubes drying tough.   On angiosperms in Fla.   Compare 24. *P. phlebiae-
     formis*.   Syn.: *ossea* Baxt.

89. *Poria mutans* Peck.   Tissue reddening then dark in KOH; tubes drying
     agglutinated, rigid.   On Castanea in the eastern U. S.

                    37b. Spores 5–8 μ long
                        40a. Tubes soft when dry

90. *Poria albobrunnea* (Rom.) Baxt.   Marginal tissue usually brown; pores 3–6
     per mm.; spores 1.5–2 μ wide.   On gymnosperms in the western U. S. and
     Canada.   Syn.: *dichroa* Bres.

91. *Poria bombycina* (Fries) Cooke.   Margin white to pale; pores 2–3 per mm.;
     spores 3–4 μ wide; color of pore surface extremely variable, usually drying
     with a lavender tint.   On gymnosperms, widely distributed.   Syn.:
     coniferarum Baxt., *fulvella* Bres.

                    40b. Tubes rigid and fragile when dry

92. *Poria aurantiaca* (Rostk.) Sacc.   More or less reddish-brown on drying.   On
     gymnosperms, of uncertain distribution.   Many different species have had
     this name applied to them; this identity is based upon Overholts'
     determinations.

93. *Poria carnicolor* Baxt.   Pink, remaining pink on drying.   On gymnosperms
     in the Pacific Northwest.

                    35b. Pore surface white to cream
                        41a. Spores ellipsoid to globose
                            42a. Sporophore membranous, rhizomorphic

94. *Poria vaillantii* (Fries) Cooke.   Spores oblong-ellipsoid, 5–7 μ long; soft
     when dry; mild.   On gymnosperms, widely distributed.

95. *Poria overholtsii* Pilát.   Spores oblong-ellipsoid, 4–7 μ long; fragile when
     dry; bitter.   On angiosperms in the eastern U. S.

96. *Poria myceliosa* Peck.   Spores short-oblong to oval, 3–4 μ long; on gymno-
     sperms, widely distributed.   Syn.: ?*consobrina* Bres., *perextensa* Murr.

97. *Poria mollusca* (Pers.) Bres.   Spores oval to subglobose, 2.5–3.5 μ long.   On
     gymnosperms and angiosperms, uncommon.

                    42b. Sporophore adnate, not membranous and not
                        rhizomorphic
                        43a. Taste bitter; on wood of gymnosperms

98. *Poria albipellucida* Baxt.   Pores 3 per mm.; annual; drying cartilaginous.
     On gymnosperms in the Pacific Northwest.

99. *Poria crassa* (Karst.) Sacc.   Pores 5–6 per mm.; perennial; waxy, drying
     waxy-chalky.   On gymnosperms, widely distributed in the northern U. S.
     and Canada.

                    43b. Taste mild; on wood of angiosperms

100. *Poria aneirina* (Sommerf.) Cooke.   Pores 1–3 per mm.   On angiosperms,
     especially Populus, widely distributed.   Syn.: *fulvescens* Bres., *macra*
     (Sommerf.).

101. *Poria distorta* Murr.   Somewhat similar to the preceding species but pores
     4–5 per mm., and context hyphae more consistently thick-walled.   Known
     only from the type from N. C. on hardwood, this an abnormal specimen.
     The sporophore may be a resupinate condition of a species of Polyporus.

102. *Poria versipora* (Pers.) Rom.   Pores 3–5 per mm.; tubes up to 2 mm. long;
     clamp connections very small; terminally inflated hyphae often present
     in hymenium.   On angiosperms, widely distributed.   Syn.: *adpressa*
     Murr., *eyrei* Bres.—cystidia reported by Bresadola not found on type,
     jalapensis Murr. *latitans* Bourd. & Galz.—allantoid spores as described
     by Bourd. & Galz. almost certainly in error, *lignicola* Murr., *ochracea*
     Murr.   See also note under 47. *P. rimosa*.

103. *Poria elongata* Overh.   Pores 3–5 per mm.; tubes up to 10 mm. long, drying
     fragile.   On angiosperms in N. Y. and Pa.

104. *Poria carnegiea* Baxt.   [Pores 3–4 per mm.; soft, arachnoid at first.
     Sporophore formed inside stems of *Carnegiea gigantea* in Arizona.]

105. *Poria elachista* (Berk.) Cooke.   Pores 5 per mm.; tubes drying waxy-fragile.
     On rotten wood in S. Car.; inadequately known from minute specimens of
     type material.   Syn.: *minima* (Rav.)

41b. Spores cylindrical, oblong or allantoid
44a. Sporophore tough

106. *Poria cinerascens* Bres. Mild; pore surface drying sordid; tissue tough-fibrous. On gymnosperms, widely distributed. Syn.: *subavellanea* Murr.; *subfuscoflavida* (Rostk.) of American determinations.
107. *Poria sequoiae* Bonar. Very similar to the preceding and perhaps a synonym. Spores as described by Bonar were not found in type material; my measurements are 3.5–4 x 1.5–2 μ, Bonar's 4.5–6 x 2–3.5 μ. Concept of species was mixed with *P. cinerascens* as shown by Bonar's determinations.
108. *Poria carbonica* Overh. Slightly resinous; pore surface white to yellowish; tissue drying waxy-tough. On gymnosperms in the Pacific Northwest.

44b. Sporophore soft, drying fragile
45a. Spores 5–10 x 1.5–3 μ

109. *Poria mappa* Overh. & Lowe. Spores 7–10 μ long. On gymnosperms in N. Y. and Brit. Col.
110. *Poria albolilacina* (Karst.) Sacc. Spores 4–6 μ long; mild. On gymnosperms, widely distributed but rare. Syn.: *microspora* Overh., *monticola* Murr.; *roseomaculata* (Karst.).
111. *Poria johnstonii* Murr. So similar to next preceding that there is a strong possibility that they are synonymous. On gymnosperms in Cal.

45b. Spores 3–5 x 1–1.5 μ

112. *Poria rancida* Bres. Spores 4–6 x 2–3 μ; pores 2–4 per mm.; bitter. On gymnosperms in the eastern U. S. Syn.: *cognata* Overh. *P. resinascens* (Rom.) Lund. & Nannf. may be the same on hardwood substrata.
113. *Poria subvermispora* Pilát. Bitter; pores 2–4 per mm.; spores 3.5–5 x 1–1.5 μ. On angiosperms and gymnosperms in Ont., N. Y., Pa., and Mo. Syn.: *notata* Overh., [?*quercuum* Baxt.].
114. *Poria vaporaria* (Fries) Cooke. Mild; pores 2 per mm. On gymnosperms, widely distributed.
115. *Poria vulgaris* (Fries) Rom. Mild; pores 4–6 per mm. On gymnosperms, widely distributed. This specific name has had varied application; the present concept agrees with Romell's determinations.

SECTION 2. SPOROPHORE SOME SHADE OF BROWN AND THE TISSUE DARKENING IN KOH SOLUTION (with the exception of 133. *Poria megalopora*).

46a. Spores distinctly brown (comparable also 137. *P. melleopora*)

116. *Poria inermis* Ell. & Everh. Spores 5–6 x 4–5 μ; pores 4–5 per mm. On Ilex and Nemopanthus in the eastern U. S.
117. *Poria umbrinella* Bres. Spores 3.5–4.5 x 2.5–4 μ; pores 6–8 per mm.; on angiosperms in the southern U. S. and tropical America. Syn.: *coruscans* (Murr.), *floridana* (Murr.), *langloisiana* (Murr.), *mexicana* (Murr.). A variable fungus, the species proposed by Murrill differing as follows: *P. coruscans* and *P. floridana* have more or less translucent tubes; *P. mexicana* has pore surface and margin dark reddish brown or varying to dark chocolate brown; *P. langloisiana* has pore surface paler, yellowish- or reddish-brown. These are not considered to be specific differences as transitions can be found.

46b. Spores greenish-yellow in mass

118. *Poria andersoni* (Ellis. & Everh.) Neuman. Sporophore formed within the outer layers of wood, these splitting off. On angiosperms in the eastern and central U. S. and in Cal. Syn.: *leei* (Murr.).

46c. Spores hyaline, or in age becoming at most pale brown
47a. Setae usually frequent to abundant
48a. Trama made up wholly or largely of setal hyphae

119. *Poria ferrugineo-fusca* Karst. Sporophore coriaceous; context hyphae nonseptate; spores allantoid, 4–5 x 1.5–2 μ. On gymnosperms, widely distributed. Syn.: *marginella* (Peck).

120. *Poria weirii* Murr. Sporophore soft and spongy; context hyphae septate; spores oval to subglobose, 4–5 x 3–3.5 μ. On gymnosperms in the western U. S.

     48b. Trama made up of ordinary hyphae
        49a. Setae large, 20–50 or more x 5–10 μ

121. *Poria ferrea* (Pers.) Bourd. & Galz. Pores 4–6 per mm.; spores cylindrical, 5–8 x 2–2.5 μ. On angiosperms, widely distributed. Syn.: *cylindrispora* Lloyd, *fulvida* (Ell. & Everh.).

122. *Fomes tenuis* Karst. Often resupinate; spores cylindrical, 6–8.5 x 1.5–2 μ; pores 2–4 per mm. On angiosperms and gymnosperms, widely distributed. Syn.: *isabellina* (Fries) Overh.

123. *Poria ferruginosa* (Schrad. ex Fries) Karst. Spores ellipsoid, 4–6 x 2.5–4 μ. On angiosperms and gymnosperms, widely distributed.

124. *Poria castletonensis* (Murr.) Sacc. & Trott. Spores ellipsoid, 3–4 x 2–2.5 μ. On wood in Jamaica.

125. *Poria palmicola* (Berk. & Curt.) Cooke. Bright reddish-brown, soft; pores 1.5–2.5 per mm.; setae subulate, 55–70 x 5–8 μ. On palm in Cuba. Known only from the type which is sterile.

        49b. Setae rarely exceeding 20 μ in length
          50a. Spores large, 8–10 x 6–7.5 μ

126. *Poria obliqua* (Pers. ex Fries) Karst. Sporophore forming within the outer layers of wood, these splitting off. On angiosperms in the eastern U. S. Forms sterile conks on living trees; after death of host fertile sporophores formed, these usually quickly destroyed by insects.

          50b. Spores smaller, not over 6 μ in longest dimension

127. *Poria punctatiformis* Murr. Spores oblong-ellipsoid, 4.5–6 x 1.5–2.5 μ; pores 6–7 per mm. On Quercus in Fla.

128. *Poria laevigata* (Fries) Karst. Spores broadly oval, 3.5–4.5 x 2.5–3.5 μ; pores 8–10 per mm.; perennial; context tissue dark reddish brown. On angiosperms, widely distributed. This is the resupinate condition of *Fomes igniarius* (L. ex Fries) Kickx; other synonyms are *P. betulina* (Murr.), *P. pereffusa* (Murr.), and *P. prunicola* (Murr.).

129. *Poria ludoviciana* (Murr.) Sacc. & Trott. As in *P. laevigata* except context tissue pale reddish brown; setae somewhat different from typical setae of *P. laevigata*. This may be a synonym of *P. laevigata*; it differs from that by very slight variations.

130. *Poria spiculosa* Cambell & Davidson. Virtually impossible to separate from *P. laevigata* by its sporophore morphology; culturally said to be quite different.

     47b. Setae lacking or rare
        51a. Spores large, 5–8 μ in largest dimension

131. *Poria punctata* (Fries) Karst. Pores 6–8 per mm.; perennial; context hyphae 3–4 μ in diam., rarely septate. On angiosperms and gymnosperms, widely distributed. This is the resupinate form of *Fomes robustus* Karst. but it occurs so regularly in the resupinate condition that it is desirable to have a name for this condition of the species. Syn.: *dryophila* (Murr.), *earleae* (Murr.), *jamaicensis* (Murr.), *juniperina* (Murr.), *laminata* (Murr.), *langloisii* (Murr.), *lloydii* (Murr.), *maxoni* (Murr.), *obliquiformis* (Murr.), *tsugina* (Murr.); *Fomes hartigii* Bres.

132. *Poria subiculosa* (Peck) Cooke. Pores 2–3 per mm.; a soft annual; context hyphae septate, variable, 2–11 μ in diam. On wood of gymnosperms in N. Y., Mich., and Colo. Rare.

133. *Poria megalopora* (Pers.) Cooke. Pores 6–8 per mm.; context tissue pale brown, olivaceous in KOH solution; spores cylindrical, 8–9 x 4 μ. On angiosperms in Ohio. Syn.: *ohiensis* (Murr.).

        51b. Spores not more than 5 μ in largest dimension
          52a. Sporophore chocolate brown

134. *Poria nigra* (Berk.) Cooke. Entire sporophore dark throughout; spores 3–5 x 2–3 μ. On angiosperms in the eastern U. S.

          52b. Sporophore yellowish- or reddish-brown
            53a. Pores 10 per mm.; spores 2.5–3 x 2–2.5 μ; setae rare

135.   *Poria flavomarginata* (Murr.) Sacc. & Trott. On wood of angiosperms in Cuba.

53b. Pores 5–7 per mm.; spores larger

136.   *Poria undulata* (Murr.) Sacc. & Trott. Spores hyaline, 3–4 x 2–3 μ; pores 5–6 per mm.; setae rare. On wood of angiosperms in Brit. Honduras.

137.   *Poria melleopora* (Murr.) Sacc. & Trott. Spores becoming pale brownish, 4–5 x 2.5–3.5 μ; pores 6–7 per mm.; setae absent. On wood of angiosperms in La. Similar to *P. umbrinella* from which it differs in having larger context hyphae and paler spores. Externally it is exactly like resupinate *Fomes johnsonianus* (Murr.) Lowe but internally differs in lacking setae and in having distinctly larger spores.

SPECIES IMPERFECTLY KNOWN
Context white or brightly colored

138.   *P. amesii* Murr. Type from N. Y. is sterile.
139.   *P. anoectopora* (Berk. & Curt.). Isotype from Cuba is sterile.
140.   *P. bracei* Murr. Type from Bahamas is a resupinate species of Polyporus.
141.   *P. cincinnati* (Berk.). Type from Ohio is resupinate *Polyporus tulipiferae* (Schw.) Overh.
142.   *P. clathrata* (Berk. & Curt.). Type from La. is an abnormal specimen.
143.   *P. conwayana* Pilát. [Unknown to me.]
144.   *P. excurrens* (Berk. & Curt.). Isotype material from Cuba is sterile; perhaps a species of Trametes.
145.   *P. favillacea* (Berk. & Curt.). Type from New England is resupinate *Polyporus abietinus* Dicks. ex Fries.
146.   *P. flavilutea* Murr. Type from P. R. is sterile.
147.   *P. hybrida*. Specimen so named in Farlow Herb. encircling stems of geranium at Ottawa is unknown to me.
148.   *P. hymeniicola* Murr. Type from Me. is resupinate *Polyporus semipileatus* Peck.
149.   *P. lacticolor* Murr. Type from Cuba is sterile.
150.   *P. lindbladii* (Berk.). Isotype at the Farlow Herb. is pileate, a species of Polyporus.
151.   *P. linearis* Murr. Type from Panama is sterile.
152.   *P. polyporicola* Murr. Type from Fla. is sterile.
153.   *P. rivulosa* (Berk. & Curt.). Type from Cuba is sterile. It resembles *P. undata* but clamps are present on the context hyphae.
154.   *P. salmonicolor* (Berk. & Curt.). Isotype (Farlow Herb.) on pine in S. Carolina has pores 3–4 per mm.; context hyphae clamped; sterile. Not a synonym of *P. spissa* as usually considered.
155.   *P. subcollapsa* Murr. Type from Jamaica is sterile.
156.   *P. subliberata* (Berk. & Curt.). Isotype from Cuba is sterile.
157.   *P. subundata* Murr. Type from Cuba is sterile.
158.   *P. tegillaris* (Berk.). Type from S. Car. is a young indeterminable specimen.
159.   *P. umbrinescens* Murr. Type from Jamaica is sterile. Murrill's description of spores is surely in error.

Context brown

160.   *P. altocedronensis* (Murr.). Type from Cuba is sterile.
161.   *P. cinchonensis* (Murr.). Type from Jamaica is sterile.
162.   *P. costaricensis* (Murr.). Type from Costa Rica is sterile.
163.   *P. cryptacantha* (Mont.). Reported from Fla.; type from Brazil is similar to *P. palmicola*.
164.   *P. demetrionis* (Murr.) Resupinate *Polyporus licnoides* Mont.
165.   *P. nicaraguensis* (Murr.). Type from Nicaragua is sterile.
166.   *P. shaferi* (Murr.). Type from Montserrat is sterile.
167.   *P. tenerrima* (Berk. & Rav.). Apparently based on cork cells of elm bark.

The number is that of the nearest preceding species number in the key.

adpressa–102
aestivale–16
alabamae–32
alachuana–75
albipellucida–98
albirosea–66
albobrunnea–90
albocincta–10
alboincarnata–9
albolilacina–110
albolutescens–82
albostygia–68
altocendronensis–160
alutacea–42
ambigua–52
amesii–138
andersoni–118
aneirina–100
anoectopora–139
arachnoidea–79
argillacea–30
asiatica–80
atrorubens–86
attenuata–12
aurantiaca–92
aurantiotingens–10
aurea–81
avellanea–3

barbaeformis–31
beaumontii–8
betulina–128
bombycina–91
borbonica–25
bracei–140
bresadolae–70
buttneri–10
byssina–22

calkinsii–4
candidissima–78
canescens–30
carbonica–108
carnegiea–104
carneopallens–13
carnicolor–93
caryae–30
castletonensis–124
cavernulosa–15
chromatica–33
chrysobapha–62
cinchonensis–161
cincinnati–141
cinerascens–106
cinereicolor–25
clathrata–142
cocos–50
cognata–112
cokeri–52
colorea–7
coniferarum–91
conferta–5

confusa–21
consobrina–96
conwayana–143
corioliformis–63
corticola–51
coruscans–117
costaricensis–162
crassa–99
cremeicolor–63
cremor–9
crustulina–33
cryptacantha–163
cubitispora–58
cuneatus–53
cylindrispora–121

decolorans–65
demetrionis–164
dichroa–90
diospyri–64
discolor–6
distorta–101
dodgei–26
dryina–9
dryophila–131

earleae–131
earlei–40
elachista–105
elongata–103
eupora–12
excurrens–144
eyrei–102

fagicola–57
fatiscens–57
favillacea–145
ferox–48
ferrea–121
ferrugineo-fusca–119
ferruginicincta–76
ferruginosa–123
fimbriatum–1
fimbriatella–14
fissiliformis–21
flaccida–61
flavicans–28
flavida–83
flavilutea–146
flavipora–23
flavomarginata–135
floridae–19
floridana–117
fragillima–78
fuligo–10
fulvella–91
fulvescens–100
fulvida–121
fulviseda–9
fulvobadia–13
fuscomarginata–7

gilvescens Amer. Aut.–30
glauca–10
grandis–82
greschikii–37
griseoalba–69

hartigii–131
herbicola–20
heteromorpha–3
holoseparans–66
holoxantha–8
hondurensis–18
humilis–20
hybrida–147
hymeniicola–148
hymenocystis–78

igniarius–128
illudens–17
incrassata–77
incrustans–20
inermis–116
inflata–49
isabellina–122

jalapensis–102
jamaicensis–131
johnsonianus–137
johnstonii–111
juniperina–131

lacerata–52
lacteimicans–19
lacticolor–149
laminata–131
laetifica–74
laevigata–128
laminata–131
langloisiana–117
langloisii–131
latitans–102
leei–118
lenis–40
lenta–2
lignicola–102
limitata–9
lindbladii–150
linearis–151
litschaueri–80
lloydii–131
ludoviciana–129
luteoalba–28
luteofibrata–83

macra–100
magnahypha–34
mappa–109
marginella–119
maxoni–131
medulla-panis–9
megalopora–133
melleopora–137

mexicana–117
microspora–110
minima–105
millavensis–60
mollusca–97
montana–40
monticola–110
mutans–89
myceliosa–96

nebulosa–65
nicaraguensis–165
nigra–134
nigrescens–67
niphodes–18
niveicolor–59
notata–113
nuoljae–69

obliqua–126
obliquiformis–131
ochracea–102
odora–44
ohiensis–133
oleagina–38
oleracea–35
omaema–7
onusta–78
ornata–7
ossea–88
overholtsii–95
oxydata–74

pallescens–22
palmicola–125
pannocincta–87
papyracea–31
parksii–60
pereffusa–128
perextensa–96
phlebiaeformis–24
pilati–30
pinea–77
placenta–73
polyporicola–152
porphyrophaea–13
proxima–55
prunicola–128
pulchella–8
punctata–131
punctatiformis–127
purpurea–70

quercuum–113

radiculosa–83
radula–11
rancida–112
regularis–79
resinascens–112
reticulata–71
rhoadsii–88
rhodella–69
rimosa–47
rivulosa–153
rixosa–26
robustus–131
roseitingens–57
roseomaculata–110
rubens–84
rufa–72

salicina–52
salmonicolor–154
saloisensis–84
salviae–51
sanguinolenta–65
semisupinus–22
semitincta–57
separans–51
sequoiae–107
serialis–48
sericeomollis–80
shaferi–166
semilis–54
sinuascens–28
sinuosa–36
sitchensis–46
spiculosa–130
spissa–74
stellae–45
stenospora–39
subacida–7
subambigua–61
subavellanea–106
subbadia–69
subcollapsa–155
subcorticola–57
subfimbriata–11
subfuscoflavida–106
subiculosa–132
subincarnata–43
subliberata–156
submollusca–79
subradiculosa–83

subrufa–85
subtilis–78
subundata–157
subvermispora–113
subviolacea–57
sulphurella–37
sumstinei–52

tacamahacae–87
taxicola–72
taxodium–61
tegillaris–158
tenella–57
tenerrima–167
tenuipora–41
tenuis, Fomes–122
tenuis, Poria–8
terrestris–60
tomentocincta–9
trachyspora–56
tsugina–131

umbrinella–117
umbrinescens–159
undata–66
undulata–136
unita–9

vaillantii–94
vaporaria–114
versatilis–15
versipora–102
vesiculosa–51
vicina–51
vincta–27
viridans–69
viridiuscula–87
vitellina–8
vulgaris–115

washingtonensis–54
weirii–120

xantha–37
xylostromatis–9

zameriensis–87
zonata–29

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